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THE CONDOR

Volume 63 November-December, 1961 Number 6

JOURNAL OF THE COOPER ORNITHOLOGICAL SOCIETY

THE CONDOR

JOURNAL OF THE COOPER ORNITHOLOGICAL SOCIETY

Published bi-monthly at Berkeley, California. Entered as second-class matter at the postoffice at Berkeley, California, May 15, 1925, under Act of Congress of March 3, 1879. Issued from the office of THE CONDOR, Museum of Vertebrate Zoology, Berkeley 4, California.

MANUSCRIPTS

Send manuscripts for publication to the Editor, ALDEN H. MILLER, Museum of Vertebrate Zoology, Berkeley 4, California, or to one of the Associate Editors, JOHN DAVIS or FRANK A. PITELKA, same address. Refer to suggestions on preparation of manuscripts for THE CONDOR on the back cover of recent issues of the journal.

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Subscription price to non-members, five dollars per volume, payable in advance. Single copies, one dollar each.

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Issued November 30, 1961

CONTENTS

PAGE

Specific Limits and Distribution of Ash-throated and Nutting Flycatchers.....*Wesley E. Lanyon* 421

Notes on the Behavior of the Scaly Dove.....*C. J. O. Harrison* 450

Breeding Biology of the Rhinoceros Auklet on Protection Island, Washington.....*Frank Richardson* 456

Timing of Annual Molt in the Glaucous Gulls of Northern Alaska.....*David W. Johnston* 474

A Study of Nesting Ant-Tanagers in British Honduras.....*Edwin Willis* 479

FROM FIELD AND STUDY

Supplemental Data on the Sex Ratio in Nestling Boat-tailed Grackles.....*Robert K. Selander* 504

Golden-winged Warbler in Southern California.....*Charles H. Richardson* and *Alice I. Richardson* 504

An Early Reference to Torpidity in a Tropical Swift.....*Thomas R. Howell* 505

Accipiter pectoralis, a Synonym of *Accipiter poliogaster*.....*William H. Partridge* 505

An Occurrence of the Laysan Albatross on the Northwestern Coast of Oregon.....*Leon A. Fredrich* 506

Flight Speeds of Some Small Birds.....*Oliver P. Pearson* 506

Tricolored Blackbirds Nesting in Jackson County, Oregon.....*Carl Richardson* 507

Association of Trogons and Monkeys on Barro Colorado.....*Ken Stott, Jr.*, and *C. Jackson Selsor* 508

Bird Records from San Luis Obispo County, California.....*Aryan I. Roest* 508

Winter Record of a Tree Sparrow in Central Alaska.....*Judith S. Weeden* and *Robert B. Weeden* 509

NOTES AND NEWS..... 510

INDEX TO VOLUME 63.....*Jane R. Durham* 512

THE CONDOR

VOLUME 63 NOVEMBER-DECEMBER, 1961 NUMBER 6

SPECIFIC LIMITS AND DISTRIBUTION OF ASH-THROATED AND NUTTING FLYCATCHERS

By WESLEY E. LANYON

This is the second in a series of reports on the genus *Myiarchus*, one of the most difficult genera of tyrannid flycatchers. An initial paper (Lanyon, 1960*a*) treated the Middle American populations of the crested flycatchers of the species *Myiarchus tyrannulus*. The findings here relate to the controversial relationship between the Ash-throated Flycatcher, *Myiarchus cinerascens* (Lawrence), of western United States and México and the Nutting Flycatcher, *Myiarchus nuttingi* Ridgway, of Middle America.

HISTORICAL BACKGROUND

A review of the fluctuating climate of taxonomic opinion that has characterized this particular complex within the genus will serve to indicate (1) the desirability of considering additional characters to discern taxonomic relationships, (2) the need for a better understanding of the variability of those morphological characters used in the past, and (3) the need for new field observations of certain critical breeding populations.

Ridgway described *Myiarchus nuttingi* (*in* Nutting, 1882) on the basis of a pair of birds collected near the Gulf of Nicoya, Costa Rica, and from additional specimens representing localities from Tehuantepec south to the type locality. He recognized the close affinity of his new species to *Myiarchus cinerascens*, a well-known form of northern México and western North America (*M. c. cinerascens*; Lawrence, 1851) and Baja California (*M. c. pertinax*; Baird, 1859), but he emphasized the smaller size of the Middle American form and the differences in the dusky patterns of its rectrices. J. A. Allen (1892) reconsidered *M. nuttingi* and found the character of the rectrix pattern quite variable and of little use in "exceptional specimens." He recommended that it be considered a smaller, southern race of *M. cinerascens*. There followed a period during which most workers (American Ornithologists' Union, 1893; Bailey, 1902; Bendire, 1895; Coues, 1903; Swarth, 1904), including Ridgway (1896), accepted Allen's interpretation.

In a collection of birds from Guerrero, Salvin and Godman (1892) found several specimens which they described as *Myiarchus inquietus*. Except for the brief notes published with the original description, *inquietus* remained comparatively unknown until the spring of 1903, when Goldman and Nelson obtained specimens at the type locality and elsewhere in southwestern México. Using their material, Nelson (1904:40) recognized that *inquietus* was intermediate in size between *cinerascens* to the north and *nuttingi* to the south. He could find no evidence of intergradation between *inquietus* and *cinerascens*, but he noted that "the specimens from the Isthmus and adjacent parts of Chiapas are distinctly intergrades showing that *inquietus* is merely a northern subspecies of *Myiarchus nuttingi*." He reinstated *M. nuttingi* to species status and considered *inquietus* to be its northern representative. Accepting Nelson's treatment of the complex, Ridgway (1907) returned to his earlier convictions and maintained *M. nuttingi* and *M. cinerascens* as distinct species, an interpretation that remained unchallenged for the next twenty years (Hellmayr, 1927).

Bangs and Peters (1928), admonishing the use of the variable rectrix pattern as a good diagnostic character, considered *inquietus* to be a "poorly marked form" and rec-

ommended its synonymy with *M. nuttingi*. Working with extensive new material from Central America, Griscom (1932) continued the recognition of *M. nuttingi* as a distinct species, but he agreed with Bangs and Peters in reducing *inquietus* to synonymy.

It was van Rossem (1931, 1932) who revived the movement to "lump" *nuttingi* (including *inquietus*) with *cinerascens*, the interpretation advocated by Allen and others forty years earlier. He advised upon the "extensive intergradation between *inquietus* and *cinerascens* in size, color, and tail markings," and furnished average measurements to demonstrate a cline from the large *Myiarchus c. cinerascens* in the north to the small *Myiarchus c. nuttingi* in the south. After working over new material from Guerrero (type locality of *inquietus*), Griscom (1934:388) agreed that van Rossem's treatment "is entirely permissible at the present time," but (p. 389) cautioned against precluding "hybridization of two different species." Van Rossem later commented (1936:115) on his own interpretation and Griscom's views: "Although [we] . . . are now in substantial agreement that *cinerascens*, *inquietus*, and *nuttingi* are conspecific, there remains considerable uncertainty as to the manner of intergradation." There were a number of workers during this period, however, who were reluctant to accept this polytypic species interpretation of the complex and who continued to follow Nelson, Ridgway, and Hellmayr in recognizing *M. nuttingi* as a distinct species (Carriker and de Schauensee, 1935; Sassi, 1939; and Wetmore, 1944).

A new race of this complex, *Myiarchus cinerascens flavidior*, was described by van Rossem (1936) on the basis of material from the Pacific lowlands of Guatemala (Griscom had called attention to the peculiarities of this population in 1932) and El Salvador.

As additional material became available, van Rossem (1945:152) reversed his stand once again and recommended that the complex be divided into the two species: "two closely related but distinct species are involved and . . . the truly impressive number of intermediates are the result of hybridization on a mass scale." At this same time, he reinstated Kaup's (1851) name, *mexicanus*, to designate the southernmost breeding populations of *M. cinerascens*. Presumably this would be the race of *M. cinerascens* principally involved in the "mass hybridization" with *M. nuttingi inquietus*.

Dickerman and Phillips (1953) suggested that the number of "hybrids" could be reduced by the use of better characters to distinguish the two species. More recently, Phillips (1960) has designated the northernmost population of *M. nuttingi* (from northwestern México) as a new race, *vanrossemi*.

The treatment of *M. cinerascens* and *M. nuttingi* as distinct species received authoritative support in the Fifth Edition of the A.O.U. Check-list (1957) and the Mexican Check-list (Pacific Coast Avifauna, 1957) although the latter recognized "hybridization of considerable extent in some areas." This interpretation has not been universally accepted, however (Sutton, 1951; Blake, 1953; Rand and Traylor, 1954; Felton and Steinbacher, 1955; Brodkorb, *in litt.*, 1960). In his unpublished manuscript on the Tyrannidae for a forthcoming volume of Peters' Check-list, Zimmer, with extensive experience in the taxonomy of this family, recognized but one polytypic species, *M. cinerascens*.

MATERIALS AND METHODS

Populations in southern Arizona were studied during the summers of 1956 and 1957. An expedition from April through June, 1959, provided firsthand knowledge of critical breeding populations in Costa Rica, Nicaragua, El Salvador, Guatemala, and southern México. A second expedition, during May, 1960, concentrated on populations in western México. Emphasis in these field studies was placed on collecting a series of specimens of known sex, vocalizations, habitat preference, and mate preference. Color of mouth

linings was noted in all fresh specimens and photographed in representative individuals. Tape recordings were made of representative vocalizations of each of the breeding populations visited, using a Magnemite recorder at 15 inches per second, a preamplifier, and an Altec 660B microphone mounted in a 24-inch parabolic reflector. These recordings involved 68 individuals of the forms being reported on here, from Costa Rica north to Arizona. All recordings were analyzed by ear in the laboratory, and subsequently over 350 representative vocal patterns were selected for analysis with a sound spectrograph. The spectrograms presented here were chosen to demonstrate the extremes of variation evident from this analysis.

Over 1200 museum specimens of this complex were examined and analyzed for morphological variation. Linear measurements, in millimeters, were taken as follows: wing, flattened; tail, from the insertion of the central rectrices; bill length, from the anterior margin of the nostril. Wing formula is expressed in terms of the length of the ninth primary relative to that of the sixth and fifth primaries. Only individuals that had completed the postjuvenal molt were included in the determination of variability of morphological characters. In diagramming statistical analyses, 1.3 times the standard deviation has been plotted on each side of the mean (forming a solid rectangle). Thus, when comparing two samples, non-overlap of the solid rectangles indicates the probability that at least 90 per cent of the individuals of one sample are separable from 90 per cent of the individuals of the other sample with respect to the particular character being analyzed.

ACKNOWLEDGMENTS

This study has been supported by research grants from the National Science Foundation (G–7083 and G–10754), the American Philosophical Society (G–2152), and the Frank M. Chapman Memorial Fund (1956). I am much indebted to Colonel and Mrs. D. S. McChesney of Syracuse, New York, for contributing immeasurably to the success of the expedition of 1959. Field work in Arizona was done, in part, at the Southwestern Research Station of the American Museum of Natural History. Permits to collect specimens in México were obtained through the courtesy of Ing. Luis Macias Arellano, Direccion General de Caza, Departamento de Conservación de la Fauna Silvestre, México, D.F.

For the loan of museum material I am grateful to the following individuals and institutions: Pierce Brodkorb; California Academy of Sciences; Chicago Natural History Museum; Cornell University; Instituto de Biologia, México, D.F.; Kansas University Museum of Natural History; Museum of Comparative Zoology; Museum of Natural History, University of Minnesota; Museum of Vertebrate Zoology, University of California, Berkeley; Museum of Zoology, University of Michigan; Allan R. Phillips; George M. Sutton; University of California at Los Angeles; University of Florida. Additional material was examined through the courtesy of: Ed N. Harrison; Thomas R. Howell; Los Angeles County Museum; Moore Laboratory of Zoology, Occidental College; William J. Sheffler; and the United States National Museum.

I am especially indebted to Allan R. Phillips and Joe T. Marshall, Jr., for their many helpful suggestions during the course of this study, and to Clay Montgomery for permission to camp at Rancho Guirocoba, Sonora.

MORPHOLOGICAL VARIATION

On the basis of evidence accumulated during this study, I recognize two species in this complex: *Myiarchus cinerascens* (Lawrence), which breeds throughout much of the western United States and the Mexican plateau (*M. c. cinerascens*) and Baja California (*M. c. pertinax*); and *Myiarchus nuttingi* Ridgway, represented in western México by

a single race (*M. n. inquietus*) and in Central America by two races (*M. n. nuttingi* and *M. n. flavidior*). I have synonymized van Rossem's *mexicanus* with *M. c. cinerascens* and Phillips' *vanrossemi* with *M. n. inquietus*.

It will be apparent from the following discussion of morphological variation that a strong case for the recognition of *M. cinerascens* and *M. nuttingi* as good species can *not* be based solely on the traditional analysis of museum specimens. A remarkable uniformity of coloration, considerable seasonal variation, lack of sexual dimorphism other than in size, and overlap in all mensural characters are factors contributing to the problem. Zimmer's treatment (MS) of the complex exemplifies the limitations of this approach. Field studies of these birds, on the other hand, revealed striking differences with regard to their vocalizations and to the color of their mouth linings. On a common breeding ground, as in central and southeastern Sonora, they are known to retain these distinctions and select mates accordingly. A series of 50 specimens of known vocal patterns and color of mouth lining, accumulated in this study, supplemented with a few additional specimens from other collectors who recorded this vital information, has been used better to interpret the variability within the extensive series of museum specimens brought together for comparative purposes. It is this combined field and museum approach that has been used to determine the specific limits for the characters analyzed here.

Color of mouth lining.—This is the most practical and most reliable morphological criterion for the specific identification of fresh specimens of this complex. I have found no evidence that this character varies geographically or sexually in either species. In my series of 50 specimens of known voice, there was 100 per cent agreement between the specific determinations based solely on color of mouth linings and those based on certain diagnostic vocal patterns. All fresh specimens of the three races of *M. nuttingi* (from Costa Rica to Sonora) had orange-colored mouth linings. All fresh specimens of *M. cinerascens* from Arizona and Sonora (none of *M. c. pertinax* were available) had "flesh-colored" mouth linings ("pale ochraceous-buff" of Ridgway, 1912). There is no evidence of hybridization and introgression of this character in the series at hand. With regard to color of mouth lining, *M. cinerascens* can be grouped with the Middle American populations of *M. tyrannulus* (Lanyon, 1960*a*) and *M. nuttingi* is placed in a group with *M. crinitus*, *M. tuberculifer*, and *M. yucatanensis* (Lanyon, MS).

Rectrix pattern.—The extent and pattern of the fuscous areas on the inner vanes of the rectrices is the most variable aspect of plumage coloration in these sibling species, as it is in Middle American *M. tyrannulus* (Lanyon, 1960*a*). In spite of this variability, the differences between the two species are of a greater magnitude and consistency than is that of any other morphological character save the color of mouth lining in fresh specimens. The following key, based solely on rectrix pattern, has been prepared from 485 specimens of *M. cinerascens* and 229 specimens of *M. nuttingi*, all adults in fresh plumage (September through February). Variability in rectrix pattern is identical in both races of *M. cinerascens*. The sample of *M. nuttingi* included specimens of both *M. n. inquietus* and *M. n. flavidior*, since rectrix patterns are identical in these races. Individuals of the nominate race of *M. nuttingi* have little, if any, fuscous area on the inner vanes of the rectrices. Consequently they are no problem to identify and have not been included in the calculation of percentages of the *M. nuttingi* sample. They all key out at a single point in the key, as indicated. The characteristic fuscous pattern of the adults of these species is not apparent in the juveniles and for this reason the key is applicable to adults only. Juveniles can be recognized readily by the presence of extensive rufous on the central pair of rectrices which is never retained after the postjuvenal

molt. Proper use of the key should separate fresh-plumaged specimens with nearly 100 per cent accuracy. The effect of wear at the tips of the rectrices of adult birds becomes critical in those individuals representing the extremes in the ranges of variability of the two species. Within the sample of fresh-plumaged adults used in devising the key, I estimated that one would have difficulty in correctly keying out approximately 15 per cent of the individuals of each species following normal rectrix wear. In both fresh and worn specimens, however, the determination should be double-checked with the use of other morphological characters. There is a tendency for females of *M. cinerascens* to have a lesser amount of fuscous in the rectrices than males, as was noted by Nelson

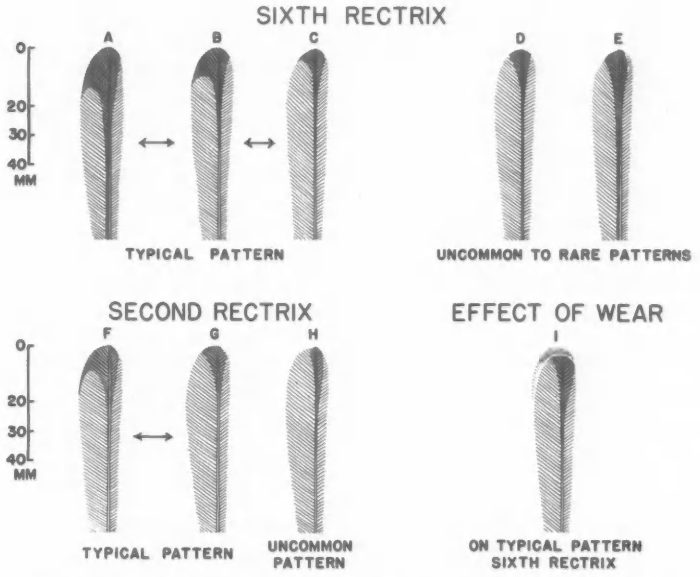

Fig. 1. Limits of individual variation in rectrix pattern of *Myiarchus cinerascens cinerascens* and *M. c. pertinax*.

(1904), although there is virtually complete overlap in this regard. No sexual dimorphism in this character could be detected in the sample of *M. nuttingi*. Presence of a character or condition on either the left or right rectrix is acceptable in the use of the key. It is important to ascertain that a specimen has the full complement of twelve rectrices, since there is a definite gradient of markings within the rectrices and this is reflected in the key's organization. Rectrices are numbered from the central pair outward. The phrase "35 mm. point" designates that point along the shaft of the feather that is located 35 mm. from the tip of the feather. Figures 1 and 2 should be consulted with the use of the key.

I. Sixth rectrix with fuscous area on inner vane expanding abruptly near the tip of the feather and often, but not always, extending forward again along the outer edge of the vane; fuscous area variable in size, but within the limits illustrated by figure 1 A-C; fuscous area not as in figure

1 D-E and figure 2 A-C; fuscous area may extend as a stripe of variable width and length along the shaft ("shaft stripe"):

A. Sixth rectrix with shaft stripe less than 1 mm. wide at the 35 mm. point.....typical *M. cinerascens* pattern; 74 per cent of sample.

B. Sixth rectrix with shaft stripe 1 mm. wide or greater at 35 mm. point:

1. Sixth rectrix with shaft stripe less than 2 mm. wide at 40 mm. point:

a. Second and/or fifth rectrix with fuscous area on inner vane as described for sixth rectrix in (I) above; usually with shaft stripe absent or less than 0.5 mm. wide at 30 mm. point of rectrices two through five.....not uncommon *M. cinerascens* pattern; 12 per cent of sample.

b. Neither second nor fifth rectrix with fuscous area as designated for sixth rectrix in (I) above; usually with shaft stripe 0.5 mm. or wider at 30 mm. point on at least one of rectrices two through five.....rare *M. nuttingi* pattern; 4 per cent of sample.

2. Sixth rectrix with shaft stripe 2 mm. wide or greater at 40 mm. point (see fig. 2 E).....rare *M. nuttingi* pattern; 3 per cent of sample.

II. Sixth rectrix without fuscous area on inner vane as described in (I) above; but rather reduced or present as a shaft stripe of variable width and length, as in figure 1 D-E and figure 2 A-C:

A. Sixth rectrix with shaft stripe less than 0.5 mm. wide at 20 mm. point (see figure 1 D) uncommon *M. cinerascens* pattern (mostly females); 9 per cent of sample. (*Myiarchus n. nuttingi*, of inland Central America, also keys out here; differs from this group of *M. cinerascens* in usually having no fuscous in inner vane of sixth rectrix, or, a trace only on that rectrix and *none* in the inner vanes of rectrices two through five; properly sexed individuals of *M. n. nuttingi* are readily separable from *M. cinerascens* on the basis of mensural characters alone).

B. Sixth rectrix with shaft stripe 0.5 mm. wide or greater at 20 mm. point:

1. Shaft stripe absent or less than 0.5 mm. wide at 30 mm. point on all rectrices two through five:

a. One or more of rectrices two through five with fuscous area on inner vane expanded within the limits shown in figure 1 F-H, but not as in figure 2 G-H.....rare *M. cinerascens* pattern (mostly females); 5 per cent of sample.

b. No fuscous area in inner vanes of rectrices two through five, or if present, as in figure 2 G-H but not within the limits shown in figure 1 F-H.....not uncommon *M. nuttingi* pattern; 19 per cent of sample.

2. Shaft stripe 0.5 mm. wide or greater at 30 mm. point on at least one of rectrices two through five.....typical *M. nuttingi* pattern; 75 per cent of sample.

I am aware of the reports of others (J. A. Allen, 1892; Nelson, 1904; Bangs and Peters, 1928) discounting the value of rectrix pattern as a diagnostic character in this complex. But I am convinced that it has been an unawareness of three factors that has led to this confusion and uncertainty: (1) the true limits of specific variability of the pattern on any given rectrix, (2) the necessity of considering the patterns of two or more rectrices in the determination of certain specimens, and (3) the effect of feather wear in altering typical patterns. Some examples will serve to illustrate these points. The abruptly-expanded fuscous pattern is characteristic of *M. cinerascens* (fig. 1 A-C). Few workers appreciate that a small percentage of *M. n. inquietus* and *M. n. flavidior* (7 per cent of my sample) also exhibit this pattern (for example, AMNH 104799 from Nayarit—"inside mouth dark orange," size and wing formula typically *M. nuttingi*; see fig. 2 D-E). The shaft stripe is characteristic of *M. n. inquietus* and *M. n. flavidior* (fig. 2 A,F), but a well developed stripe occasionally appears on the sixth rectrix of *M. cinerascens* (12 per cent of my sample; see fig. 1 A). Identification of specimens that

appear to share these species-characteristic patterns of the outer rectrix rests upon a consideration of the inner rectrices as well. Those *M. nuttingi* having an abruptly expanded fuscous pattern will also exhibit a well developed shaft stripe on the inner rectrices (fig. 2 I)—a combination not yet observed in *M. cinerascens* (fig. 1 F-H).

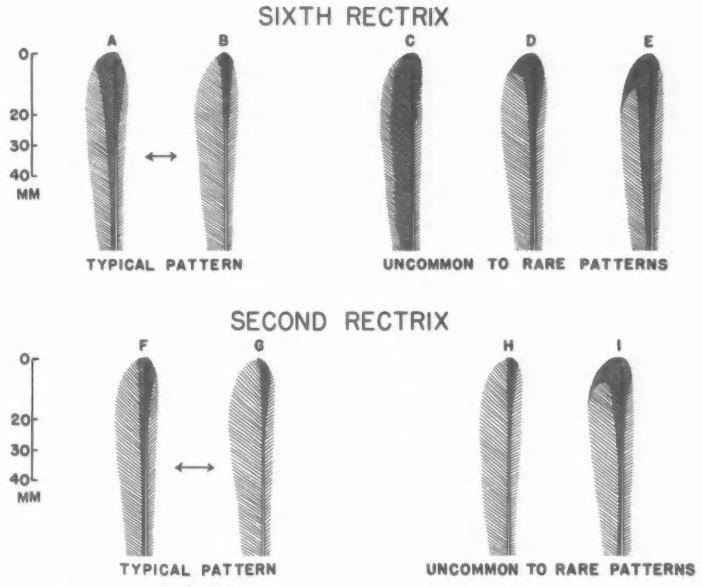

Fig. 2. Limits of individual variation in rectrix pattern of *Myiarchus nuttingi inquietus* and *M. n. flavidior*.

Another group that has puzzled workers are those *M. cinerascens* in which the sixth rectrix is without the characteristically expanded fuscous area but does have a shaft stripe (14 per cent of my sample; see fig. 1 E). The inner rectrices of these specimens may or may not have the expanded fuscous area but will *not* have a well-developed shaft stripe. Frequently in such cases, the fuscous area on the second rectrix will be reduced to a bulbous-shaped terminal pattern (fig. 1 H), thus making a distinction possible from those *M. nuttingi* having the shaft stripe reduced to a short, linear pattern terminally located (fig. 2 G-H). A typical rectrix pattern of *M. cinerascens* is sometimes transformed into something suggestive of *M. nuttingi* by the loss of a few millimeters from the tip of the rectrix, due to wear (fig. 1 I). Some badly worn specimens are thus difficult if not impossible to identify to species on the basis of rectrix pattern alone.

Except in the nominate race of *M. nuttingi*, as just noted, the considerable variability of rectrix pattern has no geographical basis. Specimens of *M. nuttingi* with characteristic vocalizations, mensural characters, and color of mouth lining, but having rectrix patterns with tendencies toward the condition in *M. cinerascens* have been taken well outside the latter's breeding range, for example, in Nayarit, Colima, and Guerrero. Similarly, specimens of *M. cinerascens* having rectrix patterns with tendencies toward the condition in *M. nuttingi* have been taken in California, Coahuila, and Nuevo León.

These instances might be interpreted by some as evidence of introgression. The specimens taken in areas of sympatry, however, show no indication of the extensive hybridization of this character that would presumably be required for such introgression. The simpler explanation would seem to be that rectrix pattern is controlled by a highly variable gene complex in both species. Admittedly, occasional hybridization would be difficult if not impossible to establish or deny on the basis of a character in which there is such a close approach in the ranges of variation within the two forms.

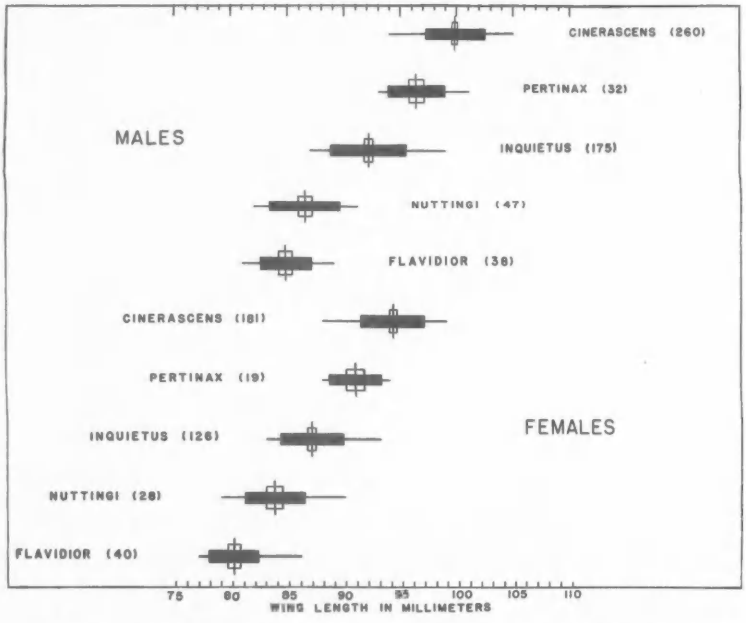

Fig. 3. Population-range diagram of wing length. Numbers in parentheses indicate sample size. Horizontal lines represent range; means are indicated by vertical lines; open rectangles indicate twice the standard error of the mean; solid rectangles indicate 1.3 times the standard deviation.

Plumage coloration.—Seasonal variation due to feather wear makes the use of plumage coloration extremely hazardous except when comparing fresh-plumaged birds. Neither species shows sexual dimorphism with regard to this character, nor is there any pronounced intraspecific variation in coloration other than rectrix pattern.

No significant divergence in plumage coloration could be detected between the two races of *M. cinerascens*. Of the three races of *M. nuttingi*, *inquietus* and *nuttingi* are indistinguishable on the basis of general coloration, whereas *flavidior* has a somewhat richer and brighter yellow abdomen. Phillips (1960) gave racial status (*vanrossemi*) to the populations of *M. nuttingi* breeding in extreme northwestern México, on the basis of their being slightly paler below and grayer above than *inquietus*. I have examined and compared 14 fresh-plumaged specimens from Sonora, including one topotypic

female, with a series of 39 fresh-plumaged specimens from Sinaloa south through Guerrero, and I am unable to recognize any consistent differences of this nature.

The following four color characters were found to be useful in differentiating *M. cinerascens* from all races of *M. nuttingi* and are given in order of decreasing effectiveness. The second character is the most transitory and is of no use in specimens taken after November. The remaining three characters are of limited value in specimens taken from December through February and are useless thereafter.

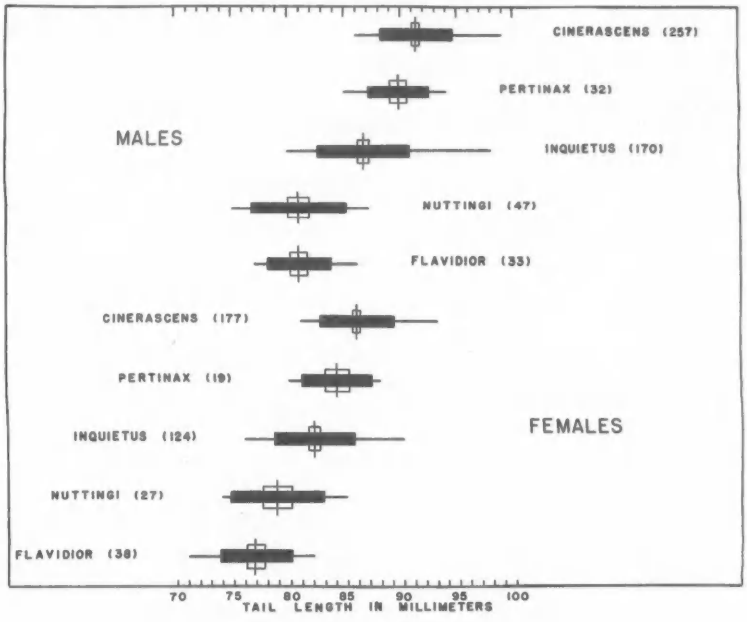

Fig. 4. Population-range diagram of tail length.

(1) *M. cinerascens* is noticeably paler below. This is most evident at the junction of the gray chest and yellow abdomen, at which point *M. cinerascens* has an extremely pale, frequently white area separating the gray from the yellow. In *M. nuttingi*, the yellow borders directly on the gray chest, rendering a more contrasty sequence of colors.

(2) *M. cinerascens* has the fringed leading edges of the secondaries whiter than those of *M. nuttingi*. In *M. cinerascens*, the deep rufous edging characteristic of the primaries is never present on the secondaries (the first secondary may be edged with a very pale rufous) and the remaining secondaries and tertials are edged with white or grayish white. In *M. nuttingi* the deep rufous edging of the primaries is always present on at least the first secondary and then fades to a pale rufous or brownish white on the remaining secondaries—only the tertials are white or grayish white. In using this character one must be careful to recognize those specimens of *M. cinerascens* that are still in the process of postjuvenal molt, for the secondaries of the juvenal plumage of that species are edged with pale rufous and would be confusingly similar to the condition found in adult *M. nuttingi*. It is not uncommon to find specimens collected as late as November and December that still retain one or two of the juvenal secondaries; for example, a specimen taken on December 18 from Guerrero (MVZ 111059)

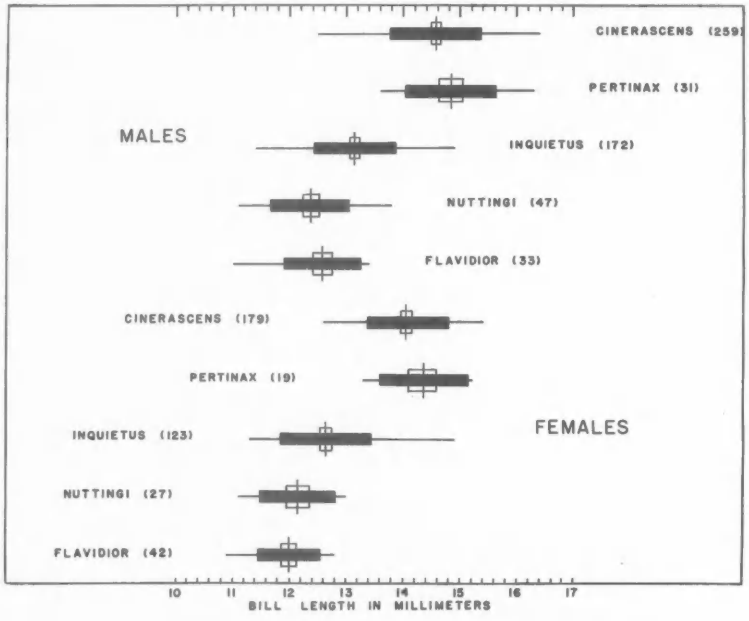

Fig. 5. Population-range diagram of bill length.

has 3 inner juvenal secondaries, and a bird from Guatemala (AMNH 395049) taken on December 5 has 2 inner juvenal secondaries. The character can be used even in these specimens, however, for the last secondaries to be replaced are the inner ones (next to the tertials). Consequently, in molting *M. cinerascens* those secondaries located adjacent to the primaries will have the white edges typical of adults.

(3) The gray of the throat in *M. cinerascens* extends dorsally as a prominent nuchal band, thus creating an area of contrast between the browner crown and back. There is no prominent nuchal band in *M. nuttingi*.

(4) The auriculars, forehead, and lores are conspicuously gray in *M. cinerascens* and brown in *M. nuttingi*.

Here again, as with the use of rectrix pattern, detection of the occasional hybrid on the basis of plumage coloration alone would be difficult if not impossible.

Wing formula.—*Myiarchus cinerascens*, the more northerly distributed and more migratory of the two species, has the more pointed wing. This correlation between migratory habit and wing shape is also reflected in a racial character that helps to differentiate *M. c. cinerascens* from *M. c. pertinax*: *pertinax*, the sedentary form in lower Baja California, has the more rounded wing. The females of both species have a more rounded wing than that of the males. To document these differences, wing formula is expressed in terms of the length of the ninth primary relative to that of the sixth and fifth primaries. Only those specimens were used in which wear had not obliterated the true relationship of these flight feathers. Table 1 summarizes the results.

TABLE 1

WING FORMULAE IN *Myiarchus cinerascens* AND *Myiarchus nuttingi*

Population	Sample size	Percentage distribution for each formula: 9 = 6 or 9 > 6	9 closer to 6 than to 5	9 closer to 5 than to 5	9 = 5 or 9 < 5
M. c. cinerascens	(429)	(67)	(32)	(1)	(0)
Males	253	79	21	0	0
Females	176	50	47	3	0
M. c. pertinax					
Males	32	34	54	9	3
Females	16	6	69	19	6
M. n. inquietus	(254)	(0)	(6)	(34)	(60)
Males	145	0	9	42	49
Females	109	0	3	22	75
M. n. nuttingi					
Males	33	0	6	36	58
Females	18	0	11	17	72
M. n. flavidior					
Males	21	0	10	42	48
Females	27	0	7	19	74

Note: Vertical lines separate the majority of *M. c. cinerascens* from *M. n. inquietus*.

Wing formula is a useful character for the specific identification of unworn specimens of this complex. It has the distinct advantage over the use of wing length (the most reliable of the mensural characters) of not being as dependent upon sex. When one compares the data in table 1 for *M. c. cinerascens* and *M. n. inquietus* (the two forms involved in sympatry), it is possible to evaluate the effectiveness of wing formula as a diagnostic character. They may be conveniently differentiated by the vertical lines shown in this table. In the samples available, 99 per cent of all *M. c. cinerascens* (regardless of sex) were thus separable from 94 per cent of all *M. n. inquietus* on the basis of wing formula alone. When the sex of a specimen is known, my samples suggest that the use of this character will separate 91 per cent of the males of *M. n. inquietus* from 100 per cent of the males of *M. c. cinerascens*, and 97 per cent of the females of *M. n. inquietus* from 97 per cent of the females of *M. c. cinerascens*.

Wing formula *per se* would be of no value in the detection of the occasional hybrid in this complex. But if, as some workers maintain, extensive hybridization occurs between *M. n. inquietus* and *M. c. cinerascens*, this condition is not reflected in wing formula according to the data in table 1. There was no significant difference in the wing formulae of the samples of the three races of *M. nuttingi*, and presumably all are about equally sedentary in habit.

Size.—The data taken on mensural characters is summarized in tables 2 and 3 and diagrammed in figures 3 to 5. Wing length had the lowest coefficient of variability of these characters. The data in figure 3 suggest the probability that at least 90 per cent of the males of *M. c. cinerascens* are separable from 90 per cent of the males of *M. n. inquietus* on the basis of wing length alone. The wing length of males averages 5 mm. longer than that of females in both species, as is the case in *Myiarchus tyrannulus* in Middle America (Lanyon, 1960*a*). Consequently, the range of variation in wing length of males of *M. n. inquietus* broadly overlaps that of females of *M. c. cinerascens*. Wing length thus constitutes a useful supplemental character in the specific determination of

individuals of this complex, providing the sex of the specimens has been accurately determined.

Although larger than *M. nuttingi* in all respects, *M. cinerascens* has a disproportionately longer wing than tail. This character, expressed here as "wing minus tail" (table 2), has the advantage of showing little, if any, sexual dimorphism. Its use, however, is of value only as a supplemental character below the population level. This wing-to-tail

TABLE 2

Measurements of *Myiarchus cinerascens* and *Myiarchus nuttingi*

Population	Wing length (mm.) Range	Mean, S.E.	S.D.	C.V.	Tail length (mm.) Range	Mean, S.E.	S.D.	C.V.	Wing minus tail (mm.) Range	Mean
M. c. cinerascens										
Males	94–105	99.9±.13(260)[1]	2.04	2.04	86–99	91.4±.16(257)[1]	2.50	2.74	3–13	8.5
Females	88–99	94.2±.16(181)	2.21	2.35	81–93	86.0±.19(177)	2.55	2.97	3–13	8.2
M. c. pertinax										
Males	93–101	96.4±.35(32)	1.98	2.05	85–94	89.8±.37(32)	2.11	2.35	4–10	6.6
Females	88–94	90.9±.41(19)	1.79	1.97	80–88	84.2±.56 (19)	2.43	2.88	4–9	6.7
M. n. inquietus										
Males	87–99	92.2±.19(175)	2.59	2.81	80–98	86.7±.24(170)	3.20	3.69	1–10	5.5
Females	83–93	87.0±.19(126)	2.14	2.46	76–90	82.1±.25(124)	2.75	3.35	0–8	4.9
M. n. nuttingi										
Males	82–91	86.5±.35(47)	2.38	2.75	75–87	80.9±.48(47)	3.26	4.03	2–10	5.6
Females	79–90	83.7±.39(28)	2.05	2.45	74–85	78.8±.61(27)	3.17	4.02	2–8	4.9
M. n. flavidior										
Males	81–89	84.8±.30(38)	1.83	2.16	77–86	80.9±.38(33)	2.18	2.69	0–8	3.9
Females	77–86	80.1±.29(40)	1.84	2.30	71–82	76.9±.39(38)	2.42	3.15	0–8	3.2

[1] Sample size.

TABLE 3

Measurements of *Myiarchus cinerascens* and *Myiarchus nuttingi*

Population	Weight (gm.) Range	Mean	Bill length (mm.) Range	Mean, S.E.	S.D.	C.V.
M. c. cinerascens						
Males	24.0–31.0	27.8(22)[1]	12.5–16.4	14.57±.04(259)[1]	.612	4.20
Females	24.5–27.8 (34.0)[2]	25.8(10)	12.6–15.4	14.05±.04(179)	.580	4.13
M. c. pertinax						
Males			13.6–16.3	14.83±.11(31)	.619	4.17
Females			13.3–15.2	14.37±.14(19)	.593	4.13
M. n. inquietus						
Males	23.8–28.2	25.8(13)	11.4–14.9	13.14±.04(172)	.562	4.28
Females	22.9–29.5	26.0(11)	11.3–14.9	12.64±.06(123)	.623	4.93
M. n. nuttingi						
Males	20.4–22.5	21.6(3)	11.1–13.8	12.36±.08(47)	.530	4.29
Females	21.7–25.7	23.9(4)	11.1–13.0	12.15±.10(27)	.505	4.16
M. n. flavidior						
Males	23.6–24.9	24.1(3)	11.0–13.4	12.58±.09(33)	.524	4.16
Females	21.5–25.2	23.2(3)	10.9–12.8	12.00±.07(42)	.430	3.58

[1] Sample size.
[2] "Laying."

ratio appears to be correlated with migratory habit, as is wing shape, for the sedentary *M. c. pertinax* has a significantly lower ratio than the nominate race. The significance of a possible similar racial difference in the case of *M. n. flavidior* is uncertain. In spite of its overall decrease in body size, *M. c. pertinax* has a slightly longer average bill length than the northern race.

Van Rossem (1945:151) recognized *M. c. mexicanus*, essentially the Mexican populations of the species, on the basis of its "slightly smaller size, proportionately slightly longer tail, and more rounded wing." When I compared a sample (61) of breeding birds from the alleged range of *mexicanus* with a sample (166) representing the northern populations of the species I found a difference of 1.5 mm. in the mean wing length of the two samples of males and a difference of only 0.8 mm. in the mean wing length of the two samples of females. These differences are less than those found between any of

TABLE 4
SUMMARY OF MORPHOLOGICAL CHARACTERS

Character	Value in specific identification	Condition in *M. cinerascens*	Condition in *M. nuttingi*	Sexual dimorphism
Color of mouth lining	Excellent, in fresh specimens only	"Fleshy"	Orange	None
Rectrix pattern	Excellent in unworn specimens; good to fair in worn birds	See fig. 1	See fig. 2	Slight, in *cinerascens*
Plumage coloration	Good in fresh plumage; no value in worn birds	a. Pale to white area between gray chest and yellow abdomen	a. Gray chest borders upon yellow abdomen	None
		b. Secondaries edged with white or grayish white	b. Secondaries edged with rufous or brownish white	
		c. Gray nuchal band	c. No nuchal band	
		d. Auriculars, forehead, lores gray	d. Auriculars, forehead, lores brown	
Wing formula (primaries)	Good in unworn birds; no value in worn birds	9th usually >6th or =6th, rarely closer to 5th than to 6th	9th usually <5th or = 5th, rarely closer to 6th than to 5th	Males average more pointed wing
Wing length	Good supplemental character in properly sexed birds	Longer; see fig. 3	Shorter; see fig. 3	Males average 5 mm. longer
Wing minus tail	Fair supplemental character	Larger wing to tail ratio; see table 2	Smaller wing to tail ratio; see table 2	None
Tail length	Fair supplemental character in properly sexed birds	Longer; see fig. 4	Shorter; see fig. 4	Males average 5 mm. longer
Bill length	Fair supplemental character in properly sexed birds	Longer; see fig. 5	Shorter; see fig. 5	Males average 0.5 mm. longer
Weight	Poor (possible specific, racial, and sexual differences masked by daily and seasonal variability)			

the other taxa in the complex. Likewise, the differences between these samples with regard to tail length, wing minus tail, and wing formula were not significant. Although, as van Rossem has correctly stated (1945), the Mexican populations do tend to be slightly smaller and exhibit the morphological adaptation of a more resident form, I believe the degree of differentiation along these lines is below the justifiable criteria for subspecific recognition in this complex.

In *M. nuttingi, inquietus* is the best differentiated of the three races on the basis of mensural characters. In Oaxaca and Chiapas, there is a rather sudden decrease in size, giving rise to the two Central American races. Of the latter, the interior *nuttingi* averages very slightly larger than the coastal *flavidior* (not *vice versa*, as reported by van Rossem, 1936).

VARIATION IN VOCALIZATIONS

Myiarchus cinerascens.—Recordings of representative vocalizations were made from breeding populations in southern Arizona (Sonoita, Santa Cruz County; Portal, Cochise County), central Sonora (about 25 miles northeast of Hermosillo), and southeastern Sonora (Rancho Guirocoba, about 30 miles east of Alamos). The two Sonoran populations were breeding sympatrically with *M. nuttingi*. Geographical variation between these populations of *M. cinerascens* was found to be no greater than the individual variation recorded within each population. The sound spectrograms shown in figures 6 and 7 were selected to demonstrate this point.

The vocal repertoire of the species consists of four basic patterns. Various combinations of these basic patterns are rendered, thus enlarging the apparent variety of the

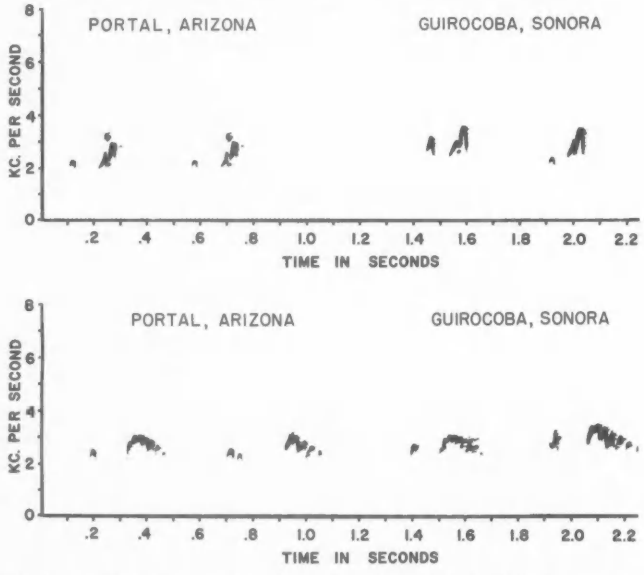

Fig. 6. Sound spectrograms of two diagnostic vocalizations of *Myiarchus cinerascens*. Neither of these calls has a counterpart in the vocal repertoire of *M. nuttingi*. Three basic patterns are represented here and a fourth one is shown in the bottom row of figure 7.

repertoire to at least six recognizably different "calls." The two most diagnostic calls, that is, those having no counterpart in the repertoire of *M. nuttingi*, are shown in figure 6. They are almost certainly the calls phonetically described in Bent (1942) as *ha-whip* and *ha-wheer*, respectively. In my field notes I have referred to the first as *ka-brick*. Each of these disyllabic calls is derived from a combination of two of the four basic vocal patterns, with three of the basic patterns all together represented in the figure. The fourth basic pattern is shown in various combinations in the bottom row of figure 7. The latter is not dissimilar to a basic pattern in the repertoire of *M. nuttingi* (see fig. 11, next to top row).

The basic pattern shown in the middle row of figure 7 is subject to some variability depending upon the level of excitement of the bird during rendition. The selection from

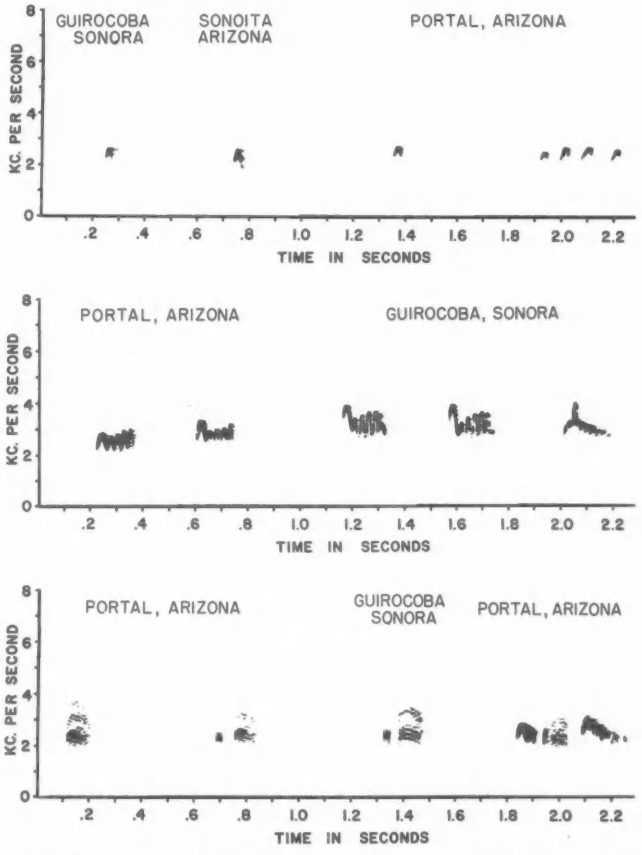

Fig. 7. Sound spectrograms of some vocalizations of *Myiarchus cinerascens*. Two of four basic vocal patterns are shown in the upper two rows. A third basic pattern appears in various combinations in the bottom row. The fourth basic pattern is shown in the top row of figure 6.

Guirocoba at the far right shows the transition to the format assumed by this pattern when used in combination with another basic pattern, as shown in the bottom row of figure 6. In this combination it becomes characteristic of only *M. cinerascens*, although

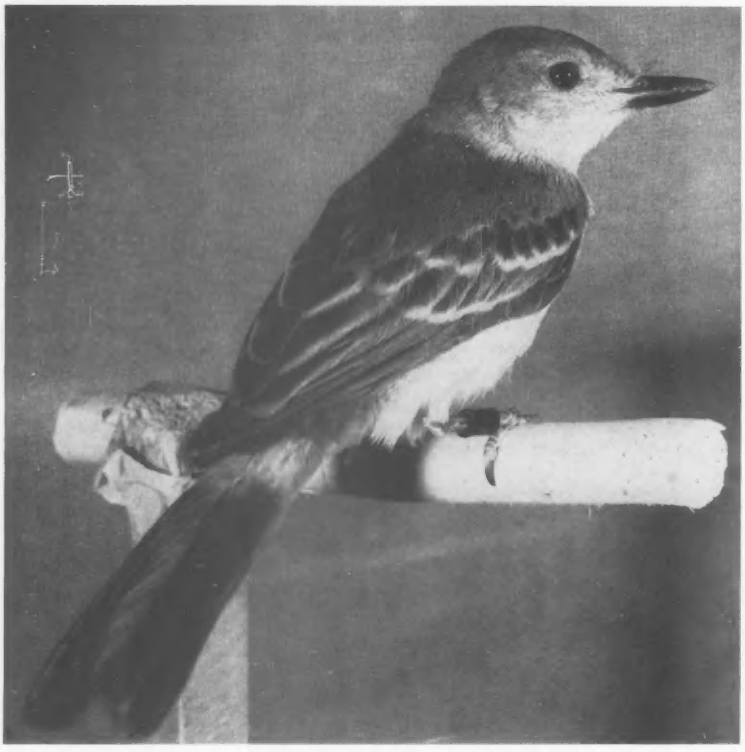

Fig. 8. Hand-reared *Myiarchus cinerascens*, photographed at 22 days of age; this bird had its species-characteristic calls as early as 16 days of age. Photograph by Willis Peterson of Phoenix, Arizona.

when rendered singly it has its counterpart in the basic repertoire of *M. nuttingi* (see fig. 11, top row).

All four of the basic vocal patterns of the species are developed in young *M. cinerascens* by the time of fledging (approximately 16 days of age). Species-characteristic calls were recorded from individuals that had been removed from a nest near Portal, Arizona, as early as six days of age and hand-reared in isolation from adults of their own species (fig. 8). This rapid development of adult vocal patterns in these hole-nesting, sub-oscine birds is suggestive of the development of the "call notes" but not of the "primary song" of those oscine species that have been studied thus far (Lanyon, 1960*b*). It may also have some bearing on the constancy of certain diagnostic calls and their reliability as species indicators throughout extensive geographical areas.

Myiarchus nuttingi.—Recordings of representative vocalizations were made from breeding populations near the following localities: Santa Cruz, Costa Rica; Jinotega, Nicaragua; La Unión and El Carmen, El Salvador; San José and Progreso, Guatemala; in México from El Camaron, Oaxaca; Acatlán, Puebla; Chilpancingo, Guerrero; Uruapan, Michoacán; Guirocoba, Sonora, and 25 miles northeast of Hermosillo, Sonora. The two Sonoran populations were breeding sympatrically with *M. cinerascens.*

The vocal repertoire of the species consists of four basic patterns. Various combinations and modifications of these basic patterns are rendered, thus enlarging the apparent

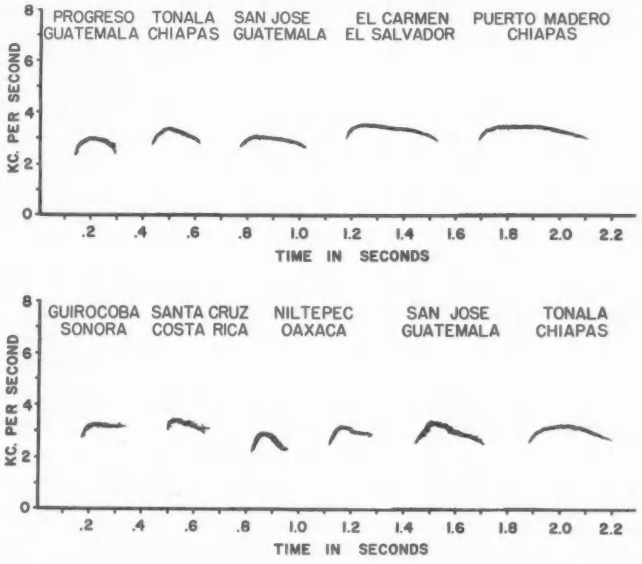

Fig. 9. Sound spectrograms of one of the basic vocal patterns of *Myiarchus nuttingi.* This diagnostic vocalization has no counterpart in the vocal repertoire of *M. cinerascens* and is an excellent character for the field identification of *M. nuttingi.*

variety of the repertoire to at least six recognizably different "calls." The most diagnostic call, that is, the one having no counterpart in the repertoire of *M. cinerascens*, is shown in figure 9. This is a clear, penetrating whistle which I have phonetically described as *peer* in my field notes. Spectrographic analysis demonstrates that it is subject to considerable variation in duration and configuration, much of which is individual in nature as illustrated in the three selections from Tonalá, Chiapas, in figure 10. When the *peer* note lasts for as long as 0.5 second, it is somewhat suggestive of the diagnostic notes of the other two "whistling species" of the genus in North and Middle America, *M. tuberculifer* and *M. yucatanensis.* It is usually at a higher frequency, however, and is more "piercing," less "sad" or plaintive to the ear. This characteristic note was recorded from all populations of *M. nuttingi* that were studied. Geographical variation between these populations was no greater than the individual variation recorded within each of the populations, as indicated by the sound spectrograms in figures 9 and 10.

Occasionally a second basic vocal pattern, somewhat similar to that of *M. cinerascens* shown in the top row of figure 7, is added as an introductory syllable to the *peer* note,

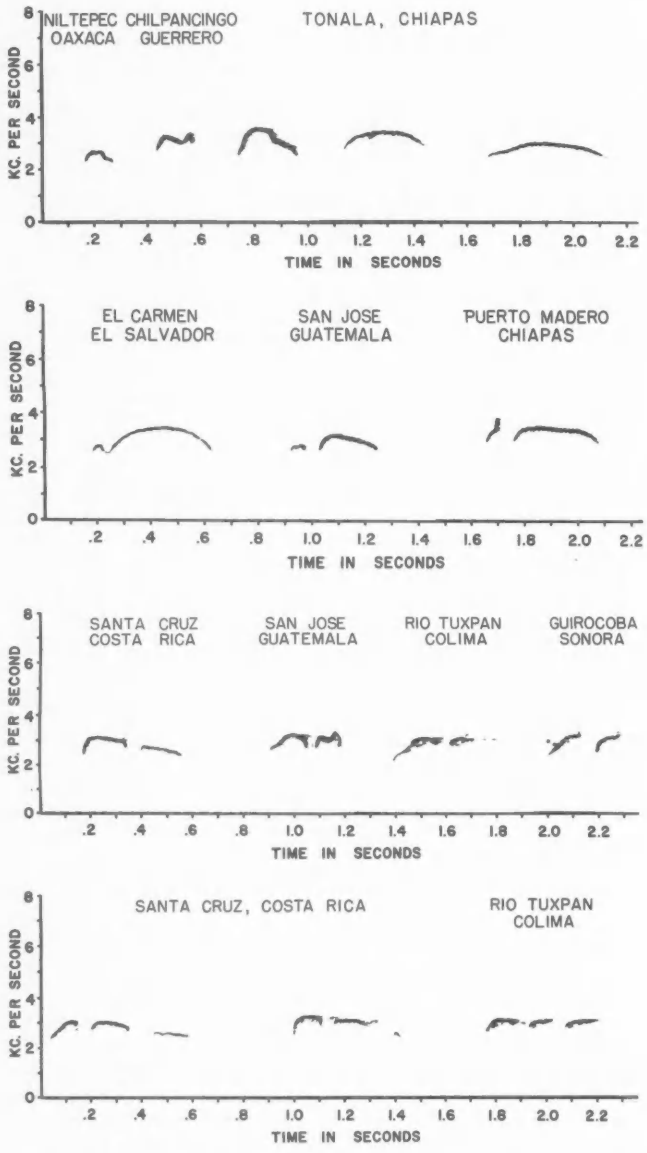

Fig. 10. Sound spectrograms of one of the basic vocal patterns of *Myiarchus nuttingi* (top row) and combinations and modifications of this basic pattern to form a variety of calls (remaining rows).

forming the *pit-peer* combination graphed in the second row of figure 10. In these calls, the "accent" or greater sound energy is consistently on the second syllable. Further variety is achieved by a repetition of the basic *peer* note, either in disyllabic or trisyllabic combinations as shown in the two lower rows of figure 10. In these calls, the "accent" is consistently on the first syllable.

The remaining two basic vocal patterns of the species are graphed in the top two rows of figure 11. Both have their counterparts in the vocal repertoire of *M. cinerascens* (see bottom two rows of fig. 7). The pattern in the top row is characteristically rendered by *M. nuttingi* in a rather nervous and repetitious manner. I have not heard it modified and combined with another basic note as is characteristically done by *M. cinerascens* (fig. 6, bottom row). The rolling call graphed in the bottom two rows of figure 11 is apparently the result of a rapid repetition of the basic pattern shown as the introductory note in the next to the top row of figure 10. Both of the other "whistling" species of *Myiarchus* in North and Middle America, *M. tuberculifer* and *M. yucatanensis*, also have a rolling call similar to this (Lanyon, MS). There is no counterpart in the repertoire of *M. cinerascens*, however.

These basic vocal patterns are apparently well developed by the time of fledging, as already noted for *M. cinerascens*. Near Progreso, Guatemala, I was photographing and recording a pair of *M. nuttingi* as they made repeated trips to their nest. By aiming the parabolic reflector toward the nest cavity, I was able to record the species-characteristic calls of the young birds within. Further examination disclosed that they were fully feathered and ready to fledge.

GEOGRAPHICAL AND ECOLOGICAL DISTRIBUTION

The breeding ranges of the forms under consideration here are indicated in a general way in figure 12. Only the localities for those breeding specimens actually examined during this study have been included.

Myiarchus cinerascens.—The Ash-throated Flycatcher is essentially a desert species and its distribution is roughly coincident with that of such well-known vegetation communities as mesquite scrub, cactus and acacia desert, creosote and sagebrush desert, and chaparral. It is also successful in riparian communities of cottonwoods, sycamores, and oaks to which it is apparently attracted by the availability of nesting cavities of suitable size rather than the accessibility of water *per se*.

The southern limits of the breeding range of *M. c. cinerascens* have never been accurately reported in the literature. The confusion arises in part from the fact that some individuals of the species are migrating (or straggling?) northward until the end of May and that many, perhaps all, juveniles and adults begin moving southward prior to the postjuvenal and postnuptial molts (Phillips, 1960). In other instances, southern breeding localities have been reported in the literature on the basis of what I consider to be misidentified specimens of *M. nuttingi inquietus*.

That at least some individuals of *M. c. cinerascens* do lag behind the main northward movement in late spring is well documented: for example, a male taken at Pijijiapan, Chiapas, on May 1, 1939 (Univ. Mich. 102602) and a "fat" female taken at Arriaga, Chiapas, as late as May 30, 1939 (Univ. Mich. 102601); a male taken on Isabel Island, Nayarit, on May 24, 1925 (Cal. Acad. Sci. 27860); a female taken at Guadalajara, Jalisco, on May 27, 1950 (Univ. Kansas 29689); and two silent males that I took at Guirocoba, Sonora, as late as May 19, 1960 (AMNH 766804 and 766805) that had fat deposits and undeveloped testes in marked contrast to the lean, breeding males collected at the same place and on the same date.

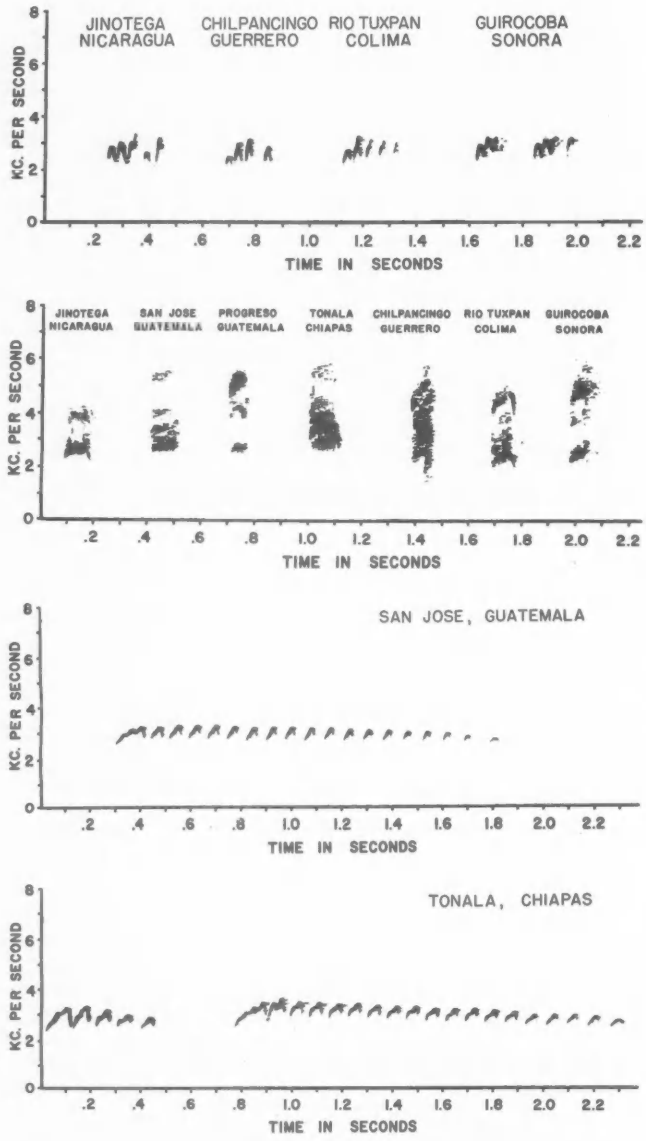

Fig. 11. Sound spectrograms of two of the basic vocal patterns of *Myiarchus nuttingi* (top two rows); a combination of a third basic pattern forms the rolling note graphed in the bottom two rows.

The contention that *M. c. cinerascens* breeds in Guerrero (Griscom, 1934; Pacific Coast Avifauna, 1957) rests mainly on a series taken by W. W. Brown near Chilpancingo, which I have re-examined. There are six *M. c. cinerascens* in this series that were taken during the latter half of May, and none of them has data on fat or gonad condition: May 15, 1943 (MVZ 110996); May 19, 1943 (MVZ 110997); May 23, 1931 (MCZ 163566, 163568, 163569) and May 27, 1941 (MVZ 111001). I worked the vicin-

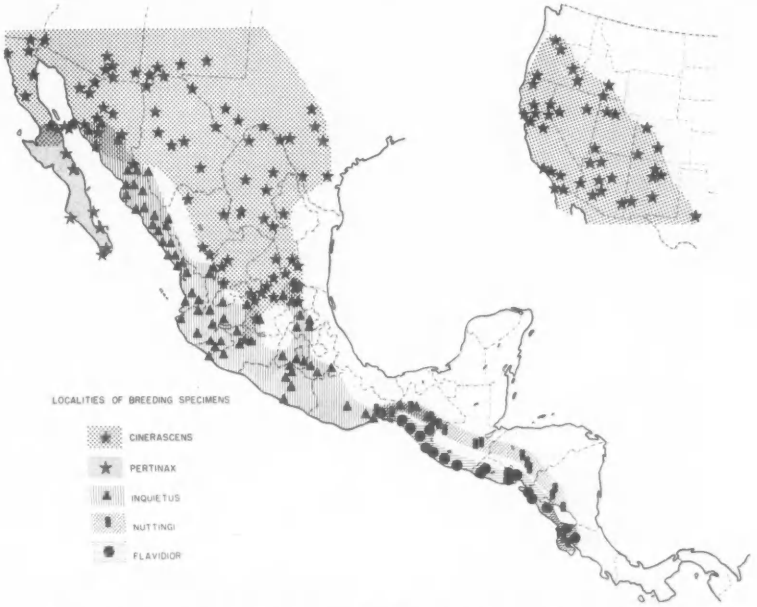

Fig. 12. Breeding ranges of *Myiarchus cinerascens* (*cinerascens* and *pertinax*) and *M. nuttingi* (*inquietus*, *nuttingi*, and *flavidior*) as indicated by localities of breeding specimens examined.

ity of Chilpancingo from May 10 to 14, 1960, and found no *M. c. cinerascens*, although *M. nuttingi inquietus* was a common breeding bird. Furthermore, the absence of a single specimen of *M. c. cinerascens* in the collections of W. W. Brown made near Chilpancingo during June and July (he took at least 21 *M. n. inquietus* from there in those months) is also significant. In view of this evidence, I think the simpler explanation is that the specimens from Chilpancingo listed previously were not breeding birds but rather late migrants or stragglers, a possibility suspected by van Rossem (1936) and considered by Griscom himself (1934:390).

The Mexican Check-list records *M. c. cinerascens* as breeding in Puebla and Hidalgo (Pacific Coast Avifauna, 1957). The evidence for Puebla rests upon two specimens in the Moore collection (57245, 57280) taken at Matamoros on May 9, 1954, and a specimen in the Sutton collection taken near Matamoros on August 14, 1952 (EPE 1545). The two specimens taken on May 9 were correctly identified as *M. c. cinerascens*: one is a female ("ovary small") and the other is a male (testes "full size"). I have examined

the specimen taken on August 14 and find it to be a male *M. nuttingi inquietus* that has nearly completed the molt. The fresh plumage permits a positive identification on the basis of rectrix pattern and plumage coloration. A specimen (Moore coll. 5353) taken by Lamb at Portezuelo, Hidalgo, on April 16, 1942, was recorded as having the testes "full size." The presence in Puebla and Hidalgo of migrating males with enlarged gonads is not unexpected at these dates which are early in view of the evidence of late stragglers already cited.

The evidence that *M. c. cinerascens* breeds at Puerto Vallarta, Jalisco (Pacific Coast Avifauna, 1957) rests on a juvenile dated June 24, and two adult males dated June 10, 1950 (Moore coll. 51149, 51150). The juvenile is too brightly colored on the abdomen to be *M. cinerascens*. The adults are correctly identified but their labels indicate that the testes were "¼ full size"; they are almost certainly late migrants or nonbreeding birds. The Mexican Check-list also states that *M. c. cinerascens* "breeds" in Sinaloa, but no specific evidence is cited. I have seen one specimen taken at Ahome, Sinaloa, on September 2, 1933 (Moore coll. 11171). It is in juvenal plumage, has been correctly identified and is, I believe, an example of the southward movement of juveniles of this species prior to the molt. I would place the same interpretation on the two specimens (AMNH 92872, 92873) taken at Escuinapa, Sinaloa, by Batty on August 6 and 16, 1904 (W. DeW. Miller, 1905) which are in postjuvenal molt. The other specimens of *M. c. cinerascens* in this collection of Batty's, which were considered by Miller as evidence that *M. cinerascens* breeds in southern Sinaloa, are clearly migrants. I have seen no specimen of this species from the Pacific lowlands of Sinaloa or Jalisco that I feel establishes its presence there as a breeding bird.

The two specimens taken by Sartorius (USNM 35126, 35127) near Mirador, Veracruz, are difficult to interpret. Although dated June, 1864, the labels read "pine forest W. of Mirador" (not an expected breeding habitat for *M. cinerascens*) and the plumage is not especially worn. Since the locality is so clearly extralimital to the known breeding range of the species, I prefer to consider these specimens as migrants, with the distinct possibility of a labeling error.

In the Pacific lowlands of México, the southern limit of the breeding range of *M. c. cinerascens* apparently coincides roughly with the juncture of mesquite desert (from the north) and tropical deciduous and thorn forest (from the south) in central and southeastern Sonora. Elsewhere in México the species is essentially confined to the plateau region. Breeding specimens from Tamaulipas have been taken from only two localities, both on the eastern edge of the plateau: for example, Miquihuana, June 7, 1898 (USNM 158785), and Jaumave, July 20, 1922 (AMNH 756584).

The southernmost breeding locality for *M. c. cinerascens*, in the material available at present, appears to be Uruapan, Michoacán. Lamb obtained a female, correctly identified to this species, on June 6, 1939 (Moore coll. 24098), and indicated that it was "nesting" (basis not given) at this locality. I visited the same area on May 14–15, 1960, and found the vegetation in the immediate environs of Uruapan to be dominantly pine. Some 20 miles southward there is a sharp drop in elevation and a narrow ecotone of pine-oak and eventually tropical deciduous forest. *Myiarchus nuttingi inquietus* was a common breeding bird in the latter community. I found no *M. c. cinerascens*. I am inclined to accept Lamb's breeding record but believe it to be extralimital to the main breeding range of the species to the north. There is a good series of specimens of *M. c. cinerascens* taken in June and July in the Moore collection that definitely establishes breeding in the vicinity of Irapuato, Guanajuato, some 90 air miles northeast of Uruapan. The main breeding populations of the plateau extend southward as far as north-

ern Jalisco (Ojuelos and Lagos de Moreno) and northern Guanajuato (Ibarra) as established by good series in the Moore collection, and extreme southern San Luis Potosí (Bledos, Villa de Reyes, and Santa María del Río) as established by good series in the Moore collection and at Louisiana State University.

Breeding specimens from Baja California indicate that *M. c. cinerascens* intergrades with *M. c. pertinax* at about latitude 29° N. *Myiarchus c. pertinax* is a resident race of the desert communities south of that latitude. After the breeding season, *M. c. cinerascens* moves southward and both races have been taken at Cabo San Lucas during the winter.

Myiarchus c. cinerascens is migratory throughout most, if not all, of its range. Wintering specimens have been taken throughout most of southern México and southward through Central America to Nicaragua and Costa Rica. The southernmost wintering specimens of this species that I have examined are a female taken at Juigalpa (Chontales), Nicaragua (T. Howell 1122) and a male taken by A. P. Smith at San Carlos, in the foothills of the Caribbean lowlands of northeastern Costa Rica (Moore coll. 13686). The specimens of "*M. c. cinerascens*" reported by Chapman (1896) as wintering in Yucatán are a male and female of *Myiarchus tyrannulus cooperi* (AMNH 66866, 66867).

Simon (1958) and Williams (1959) have summarized the records of vagrant *M. c. cinerascens* that have been taken in the United States east of the Mississippi River. Some of these specimens have been birds in juvenal plumage, additional evidence supporting movement of the species prior to the molt (as suggested previously).

Myiarchus nuttingi.—This species is essentially a resident throughout its range from central Sonora to northwestern Costa Rica. Its distribution is roughly coincident with the tropical deciduous and thorn woodlands and arid scrub of the Pacific lowlands of México and Central America and of the arid interior valleys and slopes from Chiapas southward through Nicaragua.

The range of *M. n. inquietus* extends from central Sonora to Chiapas. At the northern edge of the range a vagrant individual was taken in southern Arizona on January 8, 1952 (Dickerman and Phillips, 1953) and Phillips (1960) has interpreted Batty's specimens (AMNH 56460, 56461) from Oputo and Bacadehuachi in northeastern Sonora to be vagrants. A breeding pair (the female "ready to lay") was taken by Phillips (UCLA 33950, 33951) just west of Hermosillo on April 28, 1947. I collected both breeding adults and fledged juveniles in May, 1960, 25 miles northeast of Hermosillo, where the tropical deciduous woodland from the south penetrates into the northern mesquite desert along the Río Sonora. These are the northernmost breeding localities for the species in so far as I know.

An apparent extension of the Balsas Basin population in Guerrero and Puebla is an extensive breeding population of *M. n. inquietus* in Hidalgo and southern San Luis Potosí. Sutton and Burleigh (1941) were the first to call attention to this population, reporting on a single specimen taken at Jacala, Hidalgo, on April 12, 1939. Subsequently a good breeding series (specimens examined from the Moore collection, Louisiana State University, and University of Kansas) has been taken that confirms its presence and throws additional light on the size of the area involved (Atotonilco, Portezuelo, and Metztitlán, Hidalgo; Santa Catarina, Río Verde, Pinihuan, Canoas, Labor del Río, and other localities in southern San Luis Potosí). The northernmost specimens from this particular population that have come to my attention are a molting bird taken at Ciudad del Maíz, San Luis Potosí, on July 30, 1950 (Univ. Kansas 30036) and a male taken at Pendencia, San Luis Potosí, on November 30, 1946 (LSUMZ 11501). Attention should be called here to a series of seven specimens in the Moore collection taken during the

fall at Santo Domingo, in northwestern San Luis Potosí. I have examined them and there is no question that they are *M. n. inquietus*. There is a possibility, however, that these birds were vagrants and the status of the species at this extralimital locality remains to be determined.

The puzzling specimen (AMNH 81964) taken on May 4, 1888, near Cañon Cabelleros (just north of Ciudad Victoria), Tamaulipas, has been re-examined and is definitely a male *M. n. inquietus*. There is some indication that this may be a case of a "switch" in labels. If correctly labeled, the specimen would have to be regarded as a vagrant at best.

In the Isthmus region of Oaxaca, *M. n. inquietus* intergrades with both *M. n. flavidior* and *M. n. nuttingi*. The intergradation with *M. n. flavidior* is detectable only on the basis of size and is completed in a relatively narrow zone in eastern Oaxaca. All of the specimens that I have examined from Tonalá, Chiapas, and southward through the Pacific lowlands have been referable to *flavidior*. The intergradation of *inquietus* with *M. n. nuttingi*, recognizable by both size and rectrix pattern, is apparently accomplished over a much larger zone. The westernmost specimens of *M. n. nuttingi* examined were taken at Chivela, Oaxaca (MCZ 238286) and Tapanatepec, Oaxaca (MCZ 135543, 135552), and there is a good series of this race from the Chiapa Valley of interior Chiapas (USNM and Univ. Mich.). *Myiarchus n. inquietus* extends into the Chiapa Valley as well and has been taken as far south as Comitán (Univ. Mich. 109237) and San Vicente (USNM 193969, 193972).

Myiarchus n. flavidior breeds throughout the tropical deciduous woodland of the Pacific lowlands of Chiapas southward to northwestern Costa Rica. Its presence in Guanacaste Province, Costa Rica, is confirmed by two breeding specimens taken by A. P. Smith at Miravalles (Univ. Mich. 87583) and Las Canas (AMNH 391058) which are closer to this race than to *M. n. nuttingi*.

The range of *M. n. nuttingi* is comparatively less well known, but populations south of those in the Chiapa Valley are known from the Río Motagua in Guatemala, the Choluteca and Comayagua valleys in Honduras, the arid slopes in the vicinity of Matagalpa, Nicaragua, and the tropical deciduous woodland of Guanacaste Province, Costa Rica. In addition to the contact with *M. n. flavidior* in Oaxaca, then, there is a second zone of intergradation with that race in southern Nicaragua (?) and Guanacaste Province, Costa Rica. The majority of the specimens that I have examined from Guanacaste are referable to *nuttingi* (Ridgway's type locality was Lea Palma, Guanacaste). The material at hand is presently insufficient to determine the extent of contact, if any, between *flavidior* and *nuttingi* elsewhere in Central America other than at the northern and southern points of their ranges in Oaxaca and Costa Rica. Griscom (1932) implied that his series from the Pacific lowlands of Guatemala included two specimens of *M. n. nuttingi*. I have examined this entire series (AMNH, MCZ) and find them all to be referable to the race *M. n. flavidior*, in concurrence with the distribution suggested in figure 12.

Areas of sympatry of breeding populations.—When viewed in terms of the entire breeding ranges of the two species, the areas of sympatry during the breeding season are extremely limited in size. The rather sharp distinctions in the climate and vegetation of the respective breeding ranges suggest that the two forms have evolved differences in their ecology which now operate, in areas of contact, as partial isolating mechanisms.

Information on the overlap of the breeding ranges in central and southeastern Sonora was summarized by van Rossem (1945). The best documented Sonoran areas now known to be common breeding grounds for these species are located as follows: between Kino Bay and Hermosillo, and between Hermosillo and Ures in west-central

Sonora; immediately southeast of Guaymas and in the vicinity of San Javier in south-central Sonora; and at Guirocoba in extreme southeastern Sonora. No doubt additional localities will be found elsewhere among the poorly worked foothills of the Sierra Madre in eastern Sonora, as in the upper valleys of the Río Yaqui and Río Mayo.

Next to these areas in Sonora, the most extensive zone of sympatry during the breeding season is apparently at the southern limit of the range of *M. c. cinerascens*, in southern San Luis Potosí, northwestern Guanajuato, and northern Jalisco. Specific references have already been made to these populations. Elsewhere, as along the western edge of the central plateau, the two species seem to be ecologically isolated from one another, with *M. c. cinerascens* seldom breeding below the pine-oak or oak-juniper zones and *M. nuttingi inquietus* rarely breeding above the tropical deciduous or thorn woodlands of the lowlands. Joe T. Marshall, Jr., came to this conclusion (*in litt.*, 1959) with regard to the areas that he has worked in southern Sonora, suggesting that even in that state the degree of overlap of breeding ground may not be as extensive as implied by the observations at Guirocoba and El Gavilán. It is quite likely that where the preferred habitats merge, as for example along the upper reaches of the major rivers that drain the Sierra Madre and the plateau, the two species may breed side by side to a limited extent. J. Dan Webster (*in litt.*, 1959) has suggested such a possibility in the valley of the Río Juchipila in extreme southern Zacatecas; there he has found *M. c. cinerascens* among the cottonwoods and willows at the northern end of the valley, between Villanueva and Zacatecas City, and *M. n. inquietus* some 75 miles farther south in the tropical deciduous woodland near Moyahua.

THE QUESTION OF HYBRIDIZATION

One basic principle that I adopted early in my monographic study of the genus *Myiarchus* was that the proof for interbreeding between various populations of this complex of sibling forms must necessarily be based upon a knowledge of (1) the interactions of the respective forms on a common breeding ground, in combination with (2) the conventional morphological analysis of a museum series, rather than upon the latter alone. In other words, apparent "intergradation" between two forms in terms of one or more morphological characters does not, *ipso facto*, constitute evidence of interbreeding of those forms. From a strictly pragmatic viewpoint it would certainly be desirable if such were the case, but unfortunately these flycatchers do not lend themselves readily to this sort of treatment.

The principal "evidence" in the literature for hybridization of Ash-throated and Nutting flycatchers consists of the inferences made by Griscom (1934) in his review of W. W. Brown's material from Guerrero, and the material from Sonora that has been worked over and reviewed by van Rossem (1931, 1932, and 1945). I have already presented my case against the concept that the two species are sympatric in Guerrero. Griscom, of course, had no field experience in that region to support his morphological analysis. That his data indicate "intergradation" is not surprising in view of the availability of large samples of both species in Guerrero during the nonbreeding months and in view of the overlap or close proximity of the extremes in their variability as demonstrated in this study. One might reach the same conclusion of "intergradation" by looking at figures 3, 4, and 5, providing other criteria are ignored.

A review of van Rossem's treatment of this complex suggests the increasing significance that that veteran field worker attached to his observations of the two forms on a common breeding ground. Initially, working with a rather meager series and with the emphasis upon an intermediacy of morphological characters, van Rossem subscribed to the view that "in Sonora *cinerascens* intergrades gradually and in perfectly conven-

tional manner with *inquietus*" (1936:115). Subsequent observations made on a common breeding ground, especially at Guirocoba in 1937, gave him cause to question the simplicity of his earlier statement, yet he insisted that "the truly impressive number of intermediates are the result of hybridization on a mass scale" (1945:152).

I decided that it would be informative to re-examine, as a group, those Sonoran specimens which van Rossem had considered to be "hybrids," the "intermediate" specimens from Guerrero that puzzled Griscom, and a number of other specimens labeled "intermediate," "hybrid," or otherwise misidentified by various workers, in order to determine the morphological basis for this alleged hybridization. Many of these specimens fell within the zone of overlap between the two species with respect to wing and tail length and no doubt this was a factor contributing to the confusion. It is altogether clear now that these mensural characters cannot be used as evidence of hybridization. For example, a male specimen from Michoacán (Sutton coll., EPE 215) has a wing length of 99 mm. One worker identified it as *M. cinerascens*, presumably because of the large size and possibly because he was unfamiliar with the outer rectrix pattern, which approached the diffuse condition shown in figure 2C. However, the specimen is quite typically *M. nuttingi inquietus*, with the exception of the extreme size. Fortunately the collector had indicated on the label that the mouth lining was "dull orange." But even in the absence of that revealing information, the 9th primary is shorter than the 5th (I have yet to see a specimen of *M. cinerascens* with the wing this rounded), and the rectrix patterns and general coloration are typically those of *M. n. inquietus*. As it turned out, this was the largest specimen of *M. nuttingi* encountered in my study, but there is no reason to suspect that the explanation is anything other than individual variation.

The most obvious source of confusion over the identity of these particular specimens was an unawareness of the ranges of variability in rectrix pattern of the two species. Those individuals of *M. cinerascens* that key out at II, B, 1a in the rectrix key (only 5 per cent of my sample) are frequently misidentified or regarded as "intermediate" because that particular pattern of the sixth rectrix (fig. 1E) *does* fall within the range of variability exhibited by the pattern of the sixth rectrix of *M. nuttingi inquietus* (fig. 2A-B). But if the inner rectrices of these specimens are examined, as well as their wing formulae, the problem of identification is greatly simplified. A specimen (UCLA 31976) collected by van Rossem at Guirocoba on May 27, 1937, is a case in point. The label identifies it as a "hybrid," probably because it exhibits this particular rectrix pattern on the outer rectrix. It agrees favorably, however, with a specimen (AMNH 766806) that I took at the same locality on May 20, 1960, which had a "fleshy" mouth lining and a vocal repertoire (recorded on tape) typically that of *M. cinerascens* in all respects. Both of these specimens have the 9th primary longer than the 6th, a condition not yet observed in any specimen of *M. nuttingi*. Furthermore, a consideration of the inner rectrices (as well as the outer ones) would identify both specimens as *M. cinerascens* on the basis of rectrix pattern alone. Likewise, many workers have been unaware that the fuscous pattern on the rectrices of *M. n. inquietus* ever approaches the abruptly-expanded condition illustrated in figure 2 D,E,I (only 7 per cent of my sample) and understandably have mistaken it in some cases for the typical pattern of *cinerascens*. Again, consideration of the width of the stripe on the inner rectrices of these specimens gives the essential additional information needed for proper identification.

I spent from May 18 to May 21, 1960, at Guirocoba, Sonora, and May 22–23, 1960, at El Gavilán, 25 miles northeast of Hermosillo, Sonora. I found both species present at each of these localities, with no indication of mixed pairing and no intermediacy in the diagnostic vocal patterns or color of mouth lining. The worn plumage of the speci-

mens taken from these breeding populations precludes a discriminating analysis of intermediacy in the other morphological characters discussed previously. Nevertheless, I had no difficulty in identifying each of the specimens to species on the basis of these other characters, without recourse to the data on vocalizations or mouth lining.

I have no data on the interspecific aspects of territorialism in these areas of sympatry. Four species of *Myiarchus* breed at Guirocoba (*cinerascens*, *nuttingi*, *tyrannulus*, and *tuberculifer*) and individuals of all four can be seen and heard from any one of a number of observation points on the ranch. Marshall (1957) has commented on the lack of noticeable competition between members of this genus, in spite of "frequent occurrence together, even in the same trees," and this has been my experience in all of the areas where I have found three or four of the forms breeding sympatrically. There is some evidence that the breeding cycles of *M. cinerascens* and *M. nuttingi* are not synchronized in areas of sympatry, at least initially in the breeding season. In late May I found recently fledged young of *M. nuttingi* at both Sonoran localities, whereas the pairs of *M. cinerascens* had no fledged young but rather appeared to be still in the process of establishing territory or possibly incubating.

As I have pointed out in the discussion of morphological variation, the identification of a hybrid specimen on the basis of any one of the various characters (rectrix pattern, plumage coloration, wing formula, or body size) would be difficult if not impossible. The overlap or close proximity of the extremes of variability precludes this test. The effect of hybridization, if it occurs, upon the color of mouth lining and the characteristic vocal patterns is unknown. I can only state that to date I have not seen a specimen of this complex that could not be logically identified to species on the basis of a consideration of all the available characters. Nor have I found any correlation of intermediacy of characters or other evidence of hybridization in those specimens taken from areas of sympatry. The non-overlap in color of mouth lining and certain diagnostic vocal patterns, and the virtual non-overlap in rectrix pattern, coloration of fresh plumage, and wing formula militate against the view that there is "mass hybridization" between these forms.

SUMMARY

A combined field and museum approach has been used to determine the specific limits of various morphological and vocal characters for discriminating between Ash-throated and Nutting flycatchers. Certain diagnostic vocal patterns, color of mouth lining, rectrix pattern, and wing formula were found to be the most reliable criteria. Two species are recognized in this complex: *Myiarchus cinerascens*, which breeds throughout the western United States and the Mexican plateau (*M. c. cinerascens*), and Baja California (*M. c. pertinax*); and *Myiarchus nuttingi*, represented in western México by a single race (*M. n. inquietus*), and in Central America by two races (*M. n. nuttingi*, and *M. n. flavidior*).

The Ash-throated Flycatcher is largely a migratory species of the temperate desert and scrub communities. The southern limits of its breeding range are established for the first time, and erroneous breeding records are corrected. The Nutting Flycatcher is a resident species of the tropical deciduous and thorn woodlands. The zone of sympatry of these sibling species during the breeding season, extremely limited in area, is best documented for Sonora, southern San Luis Potosi, and northern Guanajuato and Jalisco.

The evidence for the alleged "mass hybridization" of these species is re-examined and discounted. Overlap or close proximity of the extremes of variability and an unawareness of the true specific limits of variability have caused much of the confusion in studies of this complex. Field work on two common breeding grounds in Sonora

revealed no indication of mixed pairing and no intergradation in the more diagnostic specific criteria.

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American Museum of Natural History, New York, New York, March 1, 1961.

NOTES ON THE BEHAVIOR OF THE SCALY DOVE

By C. J. O. Harrison

In a recent paper Johnston (1960) has described the behavior of the Inca Dove (*Scardafella inca*) of Central America. The behavior of the closely related Scaly Dove (*Scardafella squammata*) of South America does not appear to have been adequately described. There are two populations of this species, one in Brazil and Paraguay, and another, described as a distinct subspecies *Scardafella squammata ridgwayi*, in northern Colombia and Venezuela.

The Inca and Scaly doves have been treated as separate species (A.O.U. Check-list, 1957) and as subspecies of a single species by different authorities (Hellmayr and Conover, 1942). In such allopatric populations where the degree of relationship is uncertain and cannot be decided from structural and plumage characters, a comparative study of behavior is of value in that it makes available additional information which can be used to assess the degree of similarity and difference between the two birds.

Having kept and bred the Scaly Dove in England I have been able to record some aspects of its behavior which I think are sufficient to form a basis for comparison. Like all such studies this one suffers from the limitations of aviary conditions, where only a few individuals can be studied and movement is limited. Observations were made on seven birds. The aviary consisted of three flights, 8, 10, and 12 feet long, 3 to 4 feet wide and 6 feet high, attached to a shed allowing additional 3×4 feet shelters for two flights. No more than four birds were placed together at any one time, and when breeding occurred unmated birds were removed from the flight.

A study such as this has some advantage in that reactions may be seen in more detail than is possible in the field. It has not been possible to make a full comparison but the behavioral characters chosen are those which involve a fixed pattern of responses and which are least likely to be changed or altered by the surroundings.

In the following notes I have, for the most part, assumed that the reader is already familiar with Johnston's paper, and I have concerned myself with a comparison of the two species.

PLUMAGE

There are differences in the details of plumage coloration which make identification possible. The Scaly Dove is generally paler, being almost white on the underside, with a faint pink flush on the upper breast and head. The dark edges of the feathers are blacker and more numerous, giving a very distinct scaly pattern. The greater secondary coverts are white, showing as a broad zone of white, black-edged feathers along the lower edge of the closed wing.

This latter may have some signal value. Except when the chestnut and black coloring of the primary feathers is exposed in flight, the plumage tends to be cryptic, and I have found the doves hard to discern when, viewing them from a slight elevation, I have watched them feeding among plants and bare earth at a distance of only 25 feet. But frequently a bird will stretch the closed wings by raising them above its back, and at such times the sudden appearance of two white areas of plumage is strikingly conspicuous. I would tentatively suggest that this coloration, which is also present to a lesser degree in the Inca Dove, might serve to advertise the whereabouts of otherwise cryptically-colored birds in a species which, outside the breeding season, tends to be sociable in feeding and roosting.

VOICE

Advertisement call.—This appears to be distinct from the similar call of the Inca Dove in that it is trisyllabic—*quor-cu-cor*, the first note being very emphatic, the second short and subdued, and the third emphasized, but not as much as the first. I found the call relatively high-pitched and audible for at least one hundred yards. Goodwin (*in litt.*) compared its incisive, clear, and monotonously repetitive character to that of the call of the European Quail (*Coturnix coturnix*).

When the birds are not sexually active this call is occasionally used in circumstances where it appears to be merely self-assertive. It may be uttered, usually only once or twice, by apparently quiescent birds at almost any time. When I have heard it from a known female it has been rather higher in pitch and weaker than that of the male. I have very frequently heard it uttered at night, particularly in the breeding season. I think that at this season it is probably a self-assertive response by an awakened bird and has no special sexual significance, although it might have a functional value in alerting another bird.

The full extent to which the advertisement call is used appears to depend on the degree of sexual activity. It is used most during the nesting period and, at the beginning of each nesting cycle, the male of a pair may call incessantly for two or three hours in the early morning, although I have heard only comparatively short periods of calling at later times of day during the same part of the cycle.

Alarm call.—The alarm call of the Scaly Dove appears to be similar to that of the Inca Dove, a soft subdued *cut*. I have usually heard it uttered, not singly, but as a rapid series of notes uttered in an undertone by a mildly alarmed or nervous dove.

I would agree with Johnston that this is a "weak fear" note. He suggests that the Inca Dove shows strong fear by flying away. Captive Scaly Doves could not do so and, at the approach of a predator, even at a distance of three or four yards, uttered a "strong fear" note. This was an abrupt, loud *quok*, rather high-pitched, and repeated more frequently as fear increased. It sounded like a high-intensity version of the *cut* note, with a pitch and volume similar to that of the advertisement call. If handled, Scaly Doves utter this call note continuously and are in such circumstances the noisiest of doves.

The Scaly Dove appears to be much more sociable outside the breeding season than are other species of dove, and, while there is no evidence that the two facts are related, a loud alarm call would be of greater value to a social species than to one in which individuals were normally isolated.

In circumstances where the state of alarm of the bird appeared to be intermediate between that of "weak alarm" and "strong alarm" another note was heard, a lower-pitched, rolling *crorr*. I am not certain whether this is merely an intermediate note of alarm or whether it may have some other function.

HEAD BOBBING

Head bobbing as performed by the Scaly Dove is similar to that described for the Inca Dove but differs in some minor details. The most vigorous performance that was witnessed occurred when a male was united with a female from which he had been separated for two days. Bobbing occurred on a wooden platform in the open and it was possible to see that the male commenced by throwing back the raised head so that the bill tilted upward, after which the head described a forward and downward arc, finishing with the bill pointing downward and very near the platform. The action was rapid and was repeated a number of times in quick succession. The female responded on this occasion with a similar but less vigorous action. When this display was seen on other occasions the details were similar.

MUTUAL PREENING

I find Johnston's use of terms confusing here. I would advocate the following terminology.

A bird may either preen itself, "self-preening," or preen another bird, "heteropreening" (= mutual preening; see Carpenter, 1933). Heteropreening may be of three types. In "reciprocal preening" each bird preens the other. In "non-reciprocal preening" one bird actively preens another which is a passive recipient of the preening. This non-reciprocal preening may occur where reciprocal preening could occur if the other bird were responsive, as in the case of Carpenter's (*op. cit.*) castrate *Columba livia*. But it also occurs frequently in mixed collections of waxbills (*Estrilda* sp.) where a dominant bird is always the preener while subordinate birds are always recipients. Finally, "simultaneous preening" can occur, as in the spoonbills (*Platalea* sp.).

Johnston describes non-reciprocal preening carried over into reciprocal preening by Inca Doves. The same behavior has been noted for the Scaly Dove and it appears to be a common type of low-intensity sexual behavior in most species of dove. If one of the partners is unresponsive, the preening remains non-reciprocal. It may be initiated by either sex. In the Scaly Dove non-reciprocal preening of unmated birds was observed outside the breeding season. It was not possible to assess the degree of sexual development in the individuals concerned, but it usually occurred when an active bird joined one which was resting and preened the head of the quiescent bird. It was not possible to be certain that the birds concerned might not have established a pair bond, but if it does occur casually in this species, then it would appear to be a specific, or generic, peculiarity, possibly associated with the greater degree of sociability which appears to occur in nonbreeding birds of this genus.

Apart from the latter, it has not been possible to detect any difference in heteropreening between the Scaly Dove and other doves such as species of *Columba* and *Streptopelia*, the Diamond Dove (*Geopelia cuneata*), and *Oena capensis*, which have also been studied. Goodwin (1956*a*) has referred to apparent specific differences in the amount of preening that occurs, but since its occurrence may be related to the physiological condition of individual birds a considerable amount of quantitative data will be needed before this can be established.

VERTICAL TAIL FANNING

The display posture appears to be the same in both species of dove. I have observed a male assume this posture gradually while walking about, the tail rising in a series of jerks to become vertical and spread, while the head was lowered a little and drawn in to the shoulders. The call associated with it appears to differ in the two doves. Johnston describes tail fanning accompanied by a soft throaty call, *cut-cut-ca, doah*, which does not carry far.

In the case of the Scaly Dove the tail fanning is accompanied by two different notes. One is an abrupt, relatively high-pitched, loud *corrok*. It is similar in pitch to the advertisement call and strong alarm call and seems to be nearly as loud. In addition, interspersed between these, there is a less intense, subdued *cut* note. The tail, which is held almost vertically upward, is jerked spasmodically upward and forward at each call. At times it is almost tilted beyond the vertical, moving vigorously with each *corrok* note and less so with the *cut* note.

The two notes do not appear to be uttered in any fixed pattern. My suspicion that these may represent high- and low-intensity versions of a single call is reinforced by the fact that if a display is prolonged and the original drive begins to weaken, the proportion of *cut* notes increases, whereas the arrival of a female near a displaying male

evokes a rapid series of emphatic *corrok* notes, without the utterance of any subdued notes between them.

Throughout this irregular calling the tail is in constant jerky movement, and at times it does not appear to be wholly synchronized with the calls.

NEST CALLING

This is not recorded for the Inca Dove. The Scaly Dove shows typical nest calling behavior when the male has selected a site, prior to its recognition by the female.

In the nest calling of most of the species that I have observed the male squats on the site and calls repeatedly with a nest call which usually sounds like a modified version of the advertisement call. It is usually accompanied by some ritualized movement such as wing flicking.

The Scaly Dove differs from these species in that its nest calling closely resembles the sexual display. The male squats on the site and raises the fanned tail, although this is not normally raised so high, or fanned so completely, as in the full display. The calls uttered appear to be indistinguishable from those uttered during vertical tail-fanning.

On one occasion when a male gave the nest call on a bare twig fork in full view I was able to observe a downward thrust of the head with bill pointing downward which was repeated a number of times. It appeared homologous with the "nodding" shown by other species of dove at such times (Goodwin, 1956*a*).

AGGRESSIVE FLEEING BEHAVIOR

This is the horizontal display, and wing-up and unilateral rush, of Johnston's paper.

In simple aggression, particularly toward smaller species, as when a Scaly Dove attacked a Diamond Dove, the Scaly Dove reacts in a similar manner to the Inca Dove in "horizontal display." The head is lowered and the tail raised in a posture similar to that shown in aggressive tail-fanning of Johnston (1960, fig. 2) although I have not noticed a very marked spreading of the tail. In this posture the dove rushes directly at the object of aggression. A similar posture is adopted by a dove perching near a bird that is about to be attacked.

In writing of the "wing-up and unilateral rush" Johnston has stated that the wing-up display is a sign of aggressiveness in most pigeons and doves and that the raised wing is a signal of the intent to hit with that wing. From a study of doves in general I would question both these assertions.

In the raised-wing posture the wing farthest from the evoker of the reaction is raised and spread, and the body is aligned laterally so that a side view, with the whole upper surface of the wing displayed, is shown to the evoker.

This wing-raising posture manifests itself most frequently in situations where a bird, either through physical inability or conflicting emotional drives, is unable to escape from the approach of a predator or aggressor. In addition to its occurrence in fighting and chasing, when the drive to maintain territory probably conflicts with the desire to flee, I have seen it in partly tame, brooding adults of *Oena capensis*, *Geopelia cuneata*, and *Streptopelia chinensis*, where the urge to cover the eggs conflicted with fear at my close approach. I have also observed it in a juvenal Scaly Dove, too weak to flee, which after an initial effort squatted and raised one wing high above its back. This posture also occurred when captive Scaly Doves found themselves unable to escape when about to be caught.

Johnston describes what I consider are three good examples. He recorded this behavior from a male mounted by another male, from a feeding dove when a Black Phoebe (*Sayornis nigricans*) flew low and straight toward it, and from another dove threatened, while foraging, by a House Sparrow (*Passer domesticus*).

I would maintain that this is a type of threat display intended to intimidate the aggressor, and that it arises in a conflict situation where there is a thwarted desire to flee, the latter being indicated by the raised wing. I do not, however, consider that the raising of the wing is in itself a fleeing movement. It appears to have a similar function to the erectile dorsal fins of some fish and the head adornments of some reptiles in that it makes the bird appear, at least to a small predator, several times its original height, more difficult to attack, and a formidable opponent. Goodwin (1956*b*) suggests that it might help the bird to maintain balance when the bird strikes with the nearer closed wing.

With regard to the statement that the raised wing indicates a readiness to strike with that wing, it must be pointed out that in the cases where this display has been observed, any blows that were struck were struck with the nearer, closed wing. The lateral posture would appear to make it still more difficult for the raised wing to be of immediate effective use. It would appear that this posture is more frequent in its occurrence and more ritualized in some of the small ground doves, particularly in relation to territorial fighting, but I consider that it is homologous with the examples already mentioned and that it represents a conflict situation where a desire to flee is present. I would suggest that the horizontal display represents true aggressive behavior where no such conflict tendencies are present.

While the raising of one wing appears to indicate the presence of an ambivalent attacking/fleeing tendency, the raising of both wings appears to indicate an intention of attack. I have observed males of both the Talpacoti Dove (*Columbigallina talpacoti*) and the Scaly Dove raise both wings when pursuing another of their own species, and I have seen a male *Oena capensis*, when suddenly confronted by small estrildine waxbills in a cage, raise both wings high and partly spread the tail. Since such birds, when fighting, tend to fly onto the back of the opponent and peck at the head, the raised wings may indicate a readiness for such a movement. Goodwin (*in litt.*) has suggested that the contrasting coloration on the underside of the wings of many small doves might have a signal function in such circumstances.

It would appear to have been the latter posture that was witnessed by Evenden (1954) in the Inca Dove and mistaken for epigamic display.

Both Whitman (1919) and Goodwin (1956*b*) have described and discussed these postures, the latter referring to them under the term "defensive-threat display" to indicate the apparently conflicting drives that are evident.

DRIVING

I have not witnessed driving in the Scaly Dove, probably because mated birds were in a separate enclosure, but it may be significant that driving did not occur when a female came near a rival male separated only by a single layer of wire netting, although the two males threatened one another with lowered heads and raised tails.

Goodwin (1956*a*) stated that the purpose of driving was to remove the female from the immediate neighborhood of possible sexual rivals. He makes the suggestion that driving is a form of redirected aggression (attributed by Johnston to R. I. Smith). Johnston has criticized this on the grounds that it implies reasoning ability on the part of the male, but there appears to be no explanation as to why such a behavioral mechanism should not function innately, but with the force of the reaction governed by the recognition of the individual male against whom it was directed. Goodwin studied this behavior in individually recognized birds, and he showed that the difference in the reaction of a driving male could be related to the potential degree of sexual rivalry offered by other males. We know from the study of "peck orders" that birds are capable of recognizing individuals and varying their reaction toward them accordingly.

If redirected aggression is involved, the intensity and duration of the driving urge might indicate the degree of aggression aroused by the other male.

DISCUSSION

There seems to be relatively little difference between the two species of dove in their recorded behavior. The only definite difference is in the advertisement call and in the display call.

The differences would seem to be similar to those shown by the collared species of *Streptopelia* in Africa. There a number of species are found that differ little in plumage but have distinct call notes. In some cases there is apparent sympatry. In the case of such species, however, there appear to be ecological differences which serve to separate them. Hybridization is recorded in captivity, and where the spread of the Oriental Collared Dove (*Streptopelia decaocto decaocto*) has brought it into contact with feral stocks of the Barbary Dove (*Streptopelia risoria*) random hybridization has occurred, although the calls of the latter are different and it is thought to have been derived from the African species *Streptopelia roseogrisea*.

Using these African species as criteria one may say that the Inca Dove and Scaly Dove represent two species. While they are undoubtedly good subspecies, and while speciation is obviously occurring, I doubt whether they would at present maintain their specific identity were it not for their allopatric distribution.

SUMMARY

The behavior of the Scaly Dove (*Scardafella squammata*), recorded from captive birds, is compared with that of the Inca Dove (*Scardafella inca*), as recorded by Johnston.

There are differences in plumage coloration; the advertisement call and the display call differ; and a "strong alarm" call and nest calling were recorded for the Scaly Dove but not for the Inca Dove.

Johnston's interpretation of aggressive/fleeing behavior and driving are criticized.

The differences recorded appear similar to those found in some African species of *Streptopelia* and on these grounds the two could be considered distinct species, although it is noted that specific separation is probably not complete, the distinction being maintained by allopatric distribution.

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BREEDING BIOLOGY OF THE RHINOCEROS AUKLET ON PROTECTION ISLAND, WASHINGTON

By Frank Richardson

It is not surprising that little information can be found in the literature on the breeding cycle of the Rhinoceros Auklet (*Cerorhinca monocerata*), for this species is entirely nocturnal on its breeding islands, the young birds or incubating adults staying far within their generally deep and tortuous burrows in the daytime. This auklet, with the puffins, is structurally one of the most fossorial of the alcids (see Storer, 1945) and it is as strictly nocturnal in breeding habits as the Marbled Murrelet (*Brachyramphus marmoratum*) and Cassin Auklet (*Ptychoramphus aleutica*).

Rhinoceros Auklets have an extensive breeding range (see A.O.U. Check-list, 1957) on widely scattered islands along both shores of the North Pacific, but their southernmost breeding islands in North America, and apparently the only ones in the United States other than Alaska, are Destruction and Protection islands off the Olympic Peninsula in Washington. They once (before 1865) bred as far south as the Farallon Islands off San Francisco (Grinnell and Miller, 1944) and they have bred on Smith and Whidbey islands near Puget Sound in Washington. It was from Whidbey Island that the species and its egg were originally described, but Suckley (1859) referred to Protection Island as "a favorite breeding ground of the species where they breed in holes dug in the steep banks."

METHODS

Eighteen trips of from one to four days each were made to Protection Island in the course of four breeding seasons from 1956 to 1959. Breeding activities of auklets were observed on several parts of the island but a restricted area was chosen for more detailed study and 76 burrows were marked with posts and metal tags.

Because of the impossibility of observing much auklet activity at night—except with field glasses in moonlight—an important technique was to smooth the dirt around and in burrows and study the usually clear and numerous tracks of the auklets the next morning (fig. 4). Lights of any color frightened auklets away at night. Infrared lighting was not attempted. Flash pictures with a stroboscopic light were fairly successful.

Some 71 auklets were trapped or banded. A mousetrap fitted to a number 10 can, with loose netting at the inner end, proved most successful. Traps placed inside burrow entrances were set off by the entering auklets pushing a metal tubing roller over the end of a trigger wire. A wooden catch operated by a rubberband held the trap door shut.

Some burrows were completely opened, thus precluding future study. To allow monthly observations eight burrows were entered from behind the nest cavity and the excavations then covered. Temperatures of auklets were taken cloacally with a portable potentiometer, which instrument was also used in obtaining temperatures of burrows. A blind set up at the top of the study area was helpful in making night pictures and observations.

ACKNOWLEDGMENTS

The Department of Zoology and the Washington State Museum, both of the University of Washington, have generously allowed time for this study and helped in the preparation of this report. Research funds derived from Initiative 171 of the State of Washington are gratefully acknowledged. The chief individuals who helped with the field work were Robert Pyle, Garrett Eddy, Karl Kenyon, Howard Channing, David Johnston, Keith Macdonald, Gerald Bakus, and Virginia Richardson. Mr. Channing

was most helpful and ingenious in perfecting traps. Ashley B. Gurney identified the camel-cricket. Edward Tulin, owner of Protection Island, kindly allowed my study, and his caretakers, Roy Lynch and the late Arthur Johnson, were most gracious in helping me.

SURVEY OF PROTECTION ISLAND

Protection Island is at the eastern end of the Strait of Juan de Fuca and is about 85 miles from the open ocean. It lies at the mouth of Discovery Bay, two miles from the mainland and at 48° 08′ N latitude and 122° 55′ W longitude. The island has an area of 394 acres composed, according to Einarsen (1945), of the following land types: tillable fields, 120 acres; dense mixed coniferous woods, 82 acres; sea level sandspits, 48 acres; barren sand dunes or gravel, 44 acres; and turfed grass or pasture lands, 100 acres. The pasture land extends up the steep south and east slopes onto a plateau about 100 to 220 feet high which constitutes approximately four-fifths of the island. Roughly 30 to 35 acres of so-called pasture land that lies on steep slopes and extends back on the plateau rarely farther than 50 yards is used in varying degrees of intensity by the auklets for their burrows (fig. 1).

The coniferous woods with their associated thickets, form the chief areas of native vegetation remaining on the island. The dominant plant of the pasture land along the top of the bluff is the large perennial beach grass *Ammophila arenaria*, little grazed by domestic animals and providing much protection for auklets and their burrows. The steep slopes where over half of the auklet population breeds are largely covered with annual grasses (*Bromus rigidus* primarily, but also other *Bromus* and *Aspris* grasses). Mustard (*Brassica nigra*) is fairly common on the slopes as are also *Lepidium densiflorum*, and the gumplant (*Grindelia integrifolia*). Alfalfa plants (*Medicago sativa*) were scattered over the slopes in 1956 but are now mostly eaten down and killed by sheep. Much of Protection Island has been burned over at least twice in recent decades. Possibly this has been to the advantage of the auklets if it did not occur during their breeding season, for a dense mat of dead vegetation may form on the slopes making less ground accessible for burrowing.

Protection Island is in the rain shadow of the Olympic Mountains and, judging from data from nearby Sequim on the peninsula, averages about 16 inches of rain per year. The covering of low annual plants on slopes favored by auklets and the fairly barren spots chosen for most of their digging are attributable to the low rainfall. The slopes become very dry and brown by July.

Various land birds and a few species of sea birds breed on Protection Island but few have significant ecologic relationships with the auklets. Glaucous-winged Gulls (*Larus glaucescens*) breed chiefly on the low eastern point of the island but they are also found in fair numbers on parts of the bluffs used by auklets. Pigeon Guillemots (*Cepphus columba*) nest under rocks or logs on the beaches close below some auklets, and they occasionally nest in the cliffs. Tufted Puffins (*Lunda cirrhata*) nest on some of the same steep slopes used by auklets but select the cliff-like sections not used by the auklets for their burrows. Only the gulls may compete with the auklets for breeding space and this competition seems unimportant because of the burrowing and nocturnal habits of the auklets. The auklets hurtle close by or run around the gulls that are standing on the bluff or incubating, but apparently neither species is bothered by the other. The only instance of competition with a land bird was the taking over and enlarging of a hole of a Violet-green Swallow (*Tachycineta thalassina*) by the auklets.

The only native mammals on the island appear to be the Townsend chipmunk (*Eutamias townsendii*) and a shrew (*Sorex* sp.). Neither rats nor cats have become

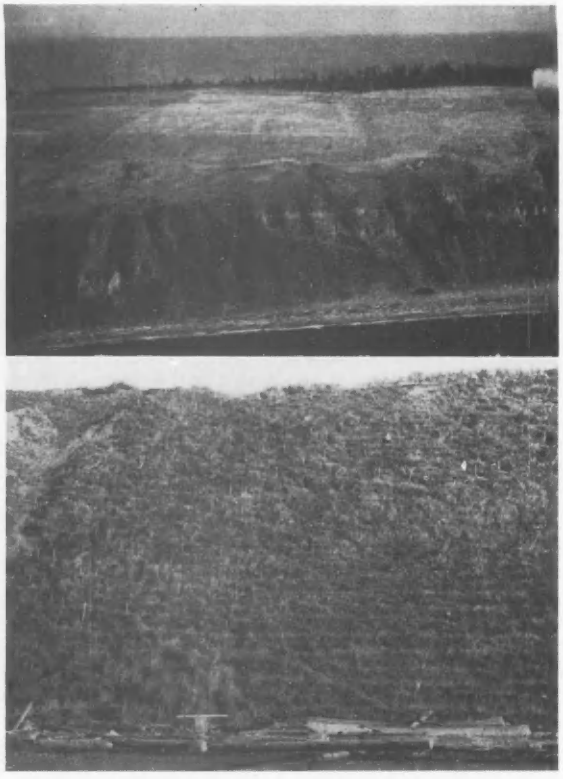

Fig. 1. Above: Oblique aerial view of center of Protection Island from the south. The study area was on the uniform steep slope in the left center foreground of the picture and in the clumps of beach grass on the dunes above. Tufted Puffins nested in some of the light-colored cliff areas. Photograph by William Calder.

Fig. 2. Below: Chief part of study area from beach. The person seated on the slope at the upper right gives an idea of the scale. Auklet burrows show up as dark spots with some of them marked by stakes. Sheep trails appear as numerous rough contour lines. Photograph by Karl Kenyon.

established but domestic ungulates have periodically been present. Since early in 1958 some 100 to 300 sheep have grazed freely over the island and are seriously affecting the breeding slopes of the auklets. Grazing, chiefly of annual grasses and what alfalfa is left, followed by frequent trampling of certain parts of the slopes as they become dry in early summer, has led to the formation of many slide areas of loose sand and soil. Auklet burrows have thus been buried in some regions and the slopes made unusable, or auklets in less severely affected areas must persistently dig out partly filled-in burrows. The seriousness of the situation is indicated by the fact that of the 76 marked burrows in the

study area, approximately 35, or 46 per cent, were buried by slides during the summers of 1958 and 1959. It was not possible to measure the mortality or renesting involved.

Sheep caved in some auklet burrows, chiefly on more level areas above the slopes. Fortunately, sheep did not graze on *Ammophila* and the many auklets nesting in this grass were not molested. After the four breeding seasons of this study, the auklet population did not seem noticeably depleted by the presence of sheep, and the auklets did not seem inclined to desert their ancestral breeding grounds. However, conditions on some slopes have become progressively worse. Increasing the number of sheep, dry years with lack of revegetation of slopes, or runoff from heavy rains, could destroy much of the best breeding areas of the auklets.

LOCATION OF AUKLET BURROWS

The auklet population on Protection Island is chiefly on or just above the steep earth slopes that extend for about 1.2 miles along the south side of the island. Burrows are scattered in the deep grass and along small hillocks as far as 75 yards back from the bluff (fig. 1). On the closely-cropped, gentle slopes at the high, west end of the island auklets breed in moderate numbers from 100 to 200 yards back from the bluffs.

Slopes under 35° were seldom used for burrows; the chief slopes used were 37° to 45°. Burrows were often located along the bases of small vertical banks but with suitable landing and takeoff slopes below them. For the nests on nearly level ground above the top of the main bluff, the auklets made use of adjacent steep slopes when taking to the wing.

Auklets usually drop a good many feet in taking off and burrows were accordingly usually 30 or more feet above the level of the beach or low-lying spits even where suitable slopes extended all the way to the bottom. However, in the study area scattered burrows were as low as six feet above and 12 feet back from the mass of logs and other flotsam marking the limit of highest water. Auklets liberated at these lowest burrows scrambled through the flotsam to take off from the water. Auklets with burrows above the spits did not nest this low down. There are fewer burrows on the southeast slope, and auklets apparently return to them later in the year. This may occur because much of this slope is above a wide spit and not directly over water.

Soil conditions and vegetation are important in determining the auklet population and its distribution on Protection Island. Although auklets are powerful diggers, soil can neither be too loose and sandy nor too hard or rocky. A rather firm, sandy soil with some roots holding it together near the surface is favored. When burrows are being started or enlarged in late winter and early spring, the ground is usually moist and easier to dig than later when it becomes dry. The problem of dry, sliding earth and sand is rarely present early in the year. Steep breeding slopes, or burrowing at the base of a small bank in a flatter area, make it possible for burrows to be dug almost horizontally and for dirt to be readily pushed out.

Early in the breeding season burrows are typically quite exposed with little vegetation around them and that mostly dead. Annual plants, chiefly *Bromus* grass, grow thickly around the burrow entrances during the spring, often partly or largely obscuring the openings. Auklets do not remove this vegetation although it may be partly buried by further removal of dirt from burrows. Most of the vegetation dies down or is grazed off during the late spring and early summer, and burrows again become exposed.

In contrast to the exposed burrows on slopes are the several hundred burrows in the *Ammophila* above the bluffs (fig. 3). Auklets make runways in this dense, high (2 to 3 feet) grass, the runways usually leading from open takeoff and landing areas on top of the bluffs.

The study area was a strip from beach to bluff-top near the center of the south side of the island (fig. 2). The area measured approximately 208 feet long and 58 to 87 feet wide, the shortest measurement being the width at the top. Seventy burrows were marked in the area. On July 13, 1957, 62 additional burrows were found in active use in the area

Fig. 3. Auklet burrow entrance in dense beach grass above bluff. Tunnels sometimes proceeded many feet in the grass before entering the subterranean burrow.

making a total of about 132 pairs of auklets in 14,040 square feet, or approximately in one-third of an acre. Heath (1915) records a much greater nesting density of up to 400 burrows in 600 square feet in dense spruce forest with little undergrowth, on Forrester Island, Alaska. Much of my study area had a maximum density of burrows, their entrances being one to three feet apart but irregularly scattered. Other parts of the area, such as the lowest part or the slightly more gently sloping (30° to 35°) central eastern part, had very few burrows. Judging from the concentration of auklets in the study area and observation of the other breeding areas, I estimated there were between 3000 and 4000 breeding pairs of auklets on the island. In addition there are indications that many nonbreeding birds are present. Thus, on Protection Island the total auklet population, including the young-of-the-year, may be well over 10,000 birds in July and early August.

NESTING

Return of adults.—The breeding grounds on Protection Island are deserted during the fall and most of the winter but by early March some auklets return and begin exca-

Fig. 4. Above: Entrance to a typical burrow on a steep slope. Note the tracks of two auklets that have left the burrow in the night. Dead *Bromus* grass is at the sides of the burrow. Photograph by Karl Kenyon.

Fig. 5. Below: Burrow entrance showing upper notch area excavated with bill. The burrow is seven inches high. Note claw scratches on surrounding hard earth. Photograph by Karl Kenyon.

vations. On March 2, 1958, the earliest visit made to the island, relatively few birds had returned and only 13 of 63 old burrows were being visited or re-excavated. On March 29, 60 of the 63 burrows were being entered. The many new burrows that were being started in late March indicated this was the time of the beginning of breeding activity for most of the auklets. Trips were not frequent enough to compare the yearly arrival time of auklets, but the comparable degree of activity of auklets in late March of three years suggests that the time does not vary greatly. Dawson and Bowles (1909) and Bent (1919) give, I think mistakenly, much later arrival dates (such as late April for De-

struction Island). Koslova (1957), however, records the return of Rhinoceros Auklets to Monyeron Island (46°N latitude, north of Hokkaido, Japan) during late March and early April.

Digging of burrows.—Digging is at its height from late March through April but it continues through July. Digging after early May cannot indicate successful nesting, for time then becomes too short for completion of the cycle. Late digging is generally for the enlargement of burrows or clearing of caved in or filled in entrances. Nevertheless, some new burrows are started, but not finished, even through July, suggesting digging as a displacement activity possibly of unmated individuals.

The auklets are very strong diggers, using both the sharply clawed, powerful feet, and the powerful bill. Initial excavations typically show a channel dug by each foot and an upper notch dug by the bill (fig. 5). Observations of digging and listening to birds digging indicate that the feet are strongly kicked backward to remove dirt from burrows. The horn on the bill is neither sharp nor stiff enough to serve in digging but it becomes partly worn down from digging with the bill.

The rate of digging, although varying with season, soil, and other factors, is somewhat predictable. Of 10 burrows started or worked on the night of March 25, 1957, and measured before and after the next night, the average increase in length was 7.6 inches (maximum 13 inches and minimum 2 inches). Two barely started burrows in the same area were not returned to this night, but observations indicate that most auklets work nightly to complete a burrow once it is started. The visits to the island were not long enough to judge accurately the time needed to complete a burrow, but I estimate that one to two weeks suffice to excavate a burrow of the usual length of six to eight feet. No visible differences between the two sexes of Rhinoceros Auklets were noted, but the worn condition of the bills and horns of most birds trapped or dug out indicates that both sexes take part in excavation of burrows.

Nature of the burrows.—Auklet burrows have been described and illustrated by Heath (1915) and Young (1929). Heath recorded burrows on Forrester Island of from eight feet to 20 feet in length, and Young states that burrows on Pine Island in Queen Charlotte Sound were six to 25 feet long but averaged 10 to 15 feet in length. On Protection Island burrows were generally shorter, perhaps because of deep compact soil, with extremes of four to 15 feet and an average of from six to eight feet in length. Some burrows did not have the blind side passage described as usually present, but the nest cavity or wide parts of the burrow would still allow mates to pass.

Occasional young Glaucous-winged Gulls seeking refuge in burrow entrances were the only other vertebrates found in auklet burrows. The most common invertebrate found, abundant even in the innermost ends of many burrows, was the camel-cricket (*Ceuthophilus agassizii*). Other invertebrates found a number of times in burrows were earwigs (*Forficula* sp.), carrion beetles (*Nicrophorus* sp.), carabid beetles, ants, spiders, and isopods (sow bugs). Generally these occurrences seemed incidental but the crickets and sow bugs appeared to live regularly in the auklet burrows.

Retention of burrows; pair bonds.—The same burrows may be used year after year or new ones may be dug nearby. Of 76 burrows in use in 1957, at least 57 were used in 1958 and 32 in 1959. Much of this reduction in use was due to burrows being caved in or buried by sheep. Banding returns of six birds showed that three returned to the same burrow a year later. Two of the six birds returned a year later, and one two years later, to adjacent burrows, the original burrows having been caved in or buried. One bird occupied three different burrows in three years; the third burrow was adjacent to the first. Other returns showed that one auklet moved from a disturbed burrow to a new one some 50 feet away and was still there the third year.

Banding returns, although few, indicated that auklets maintain the same pairs year after year. Direct evidence of pair formation early in the breeding season and indirect evidence of both members working on the burrows was afforded by observations of birds arriving at or leaving the breeding grounds. For instance, between 4:45 and 5:10 a.m., March 27, 1957, 75 auklets were counted leaving the study area and of these 68 were paired, each pair flying away close together. On this same date one auklet was seen to leave a burrow in which its mate remained.

Nest and egg.—The nest chamber, although variable, is typically an enlarged cavity at the end of the burrow. It has been described as seven to eight inches high and a foot or more across by Dawson and Bowles (1909). The last few feet of the burrow tend to slope down toward the chamber and there is often a drop-off of an inch or two from the end of the burrow into the chamber.

The nest varies from a depression in the dirt with or without a little dry grass (Young, 1929) to a shallow accumulation of available plant material such as spruce twigs, salmonberry branchlets, moss, or fern (Heath, 1915). On Protection Island only dry or green grass was found to make up nests. During the nestling period, dry grass was often added to the nest or was found in the burrows.

The single egg of the Rhinoceros Auklet has been described by Dawson and Bowles (*op. cit.*). Apparently a second egg may be laid if the first is destroyed; this probably accounts for fresh eggs found as late as June 7 by Young (*op. cit.*). The start of egg laying off southern Alaska is given as June 1 by Heath (*op. cit.*) and the last week in May by Willett (1915). Young (*op. cit.*) gives the period of May 10 to 21 for egg laying just north of Vancouver Island, and Dawson and Bowles (*op. cit.*) record egg laying on May 1 for Destruction Island. Thus there appears to be some correlation between lower latitude and earlier laying. However, on more southerly Monyeron Island north of Japan, Koslova (1957) found the first auklet eggs in early May, and on Protection Island I found eggs as early as April 21 although most are probably laid about the second week in May. On May 19, 1957, for instance, of six burrows opened, all had an egg, whereas on May 3, 1958, only one of four occupied burrows had an egg. A fresh egg was found as late as May 31.

Incubation.—The incubation period is given as about three weeks by Heath (1915) and about a month by Young (1929). Three records of eggs in the present study showed the incubation period to be over 31 days, and the nearly successful artificial incubation of one egg indicated a period of about 31 days. Occasionally eggs may hatch in late May but usually the time of hatching is in the second and third week in June. A few birds were still incubating on June 20, 1957.

There is little doubt that both males and females incubate. In several instances pairs were banded in burrows known to contain eggs. Also, there was a great deal of nightly activity of adults during the weeks of incubation. Large numbers of auklets came in at dark, many staying on the slopes during the night but many others coming or going. Almost all burrows were entered nightly and tracks in the morning almost invariably showed a bird had left the burrow. The dawn flight of auklets leaving the study area on May 19, 1957, consisted of only 22 birds, none in pairs. Such flights suggested that many birds were incubating and that the time of changing of mates was irregular.

Heath (1915) speaks of incubating auklets changing places at about 10:00 p.m. and again early in the morning, the relieved birds thus being free to go to sea to feed during the night. My studies did not indicate any such regular shift. Instead, large numbers of auklets were present on the breeding slopes throughout the night. A check of 23 traps on each of two nights during the incubation season disclosed that traps were entered

at irregular times chiefly between 10:00 p.m. and 3:00 a.m. An average of only 30 per cent of the traps were entered, suggesting that mates do not change places every night. However, the fact that most burrows without traps were entered indicates that traps often deter birds. No fish were brought into burrows in April and May, indicating that incubation was still continuing and that auklets were not bringing food to their mates.

Temperatures of birds and burrows.—A limited number of temperatures of auklets, taken cloacally with the same potentiometer and electrodes, were recorded. Two readings of adult, incubating birds were 102° and 103.5° F., low temperatures compared to most species of birds. Temperatures of young birds showed considerable variation but also indicated well-established temperature control at hatching or soon thereafter. The temperature of one young (1 to 3 days old) was 103.5° F. and of another young (4 to 6 days old) was 104.0° F. Young auklets are thus precocial in acquiring temperature control although their behavior is nidicolous during growth.

The temperature within burrows, near or in the nest chamber, remains nearly constant in spite of fluctuations outside. For instance, the temperature within one burrow was 63.5° F. when the temperature outside was 62.5° F. and the temperature within another burrow was 64.0° F. when the temperature outside was 74.0° F. The importance of the deep burrow in protecting young birds or incubating adult auklets from excess cold or heat is thus suggested. Apparently there is little or no brooding of the nestling, a fact which can be correlated both with the uniform mild temperature of the burrow and with the early establishment of temperature control in the young.

Growth of young.—The two most readily detectable signs of hatching of young are the parents bringing in fish and the frequent appearance of egg shells or membranes, presumably brought out by a parent, near entrances of burrows.

The growth of the young from hatching to fledging apparently takes five to six weeks. During that time the completely downy nestling of about 50 grams becomes a fully feathered fledgling of over 400 grams. Too few repeated weights of young birds were obtained to give an adequate idea of the growth rate, but the data in table 1 give some indication.

TABLE 1

WEIGHTS OF YOUNG AUKLETS

Young	1st weight (gm.)	Age	2nd weight (gm.)	Days later	Gain in weight (gm.)
No. 1	69.5	1–3 days	355.5	24	286.0
No. 2	95.0	4–6	410.0	24	315.0
No. 3	208.0	8–11	401.0	27	193.0

Young no. 3 appeared nearly fledged at its last weighing.

Data from table 1 and other weights recorded indicate that the rate of increase in weight of nestlings averages over 10 grams a day during the first three or four weeks but decreases greatly during the last week or two when the juvenal plumage is being completed. The young at fledging weigh a little over 400 grams, which is markedly below adult weight; the average weight of 13 adults was 542 grams with a range from 490 to 610 grams.

The young as they grow apparently move about more and more freely in the burrows. Young are ambulatory on hatching but were not actually seen in the outer part of burrows until nearly fledged. There is a lack of excrement in nest chambers but it frequently occurs outside entrances, where its forceful expulsion has been heard at night. It may occur on the walls of burrows, indicating that both young and adults usually leave the nest chamber to defecate.

The nearly grown young (figs. 6, 7) still has some patches of down attached to its teleoptiles; the down occurs chiefly on the rump, neck, and on the breast. The horn on the bill is extremely small in very young birds, but it becomes more noticeable (about ⅛ inch high) as the nestlings grow. The horn is rounded, slightly movable from side to side, and appears to be covered with skin.

Bent (1919) and others give details on plumage changes in the young but some data may be added here. The first visible changes from the completely downy plumage occur

Fig. 6. Ventral view of young auklet about four weeks old showing the large amount of down still attached to underlying contour feathers. Young were temporarily removed from burrows for photographing.

early in the fourth week when primaries and secondaries and their greater coverts are just emerging from their now conspicuous (13–18 mm.) periderm sheaths. Within two to four days of this time, areas of contour feathers appear around the bill and eye. Soon after this, at about four weeks of age, contour feathers previously developing, but hidden under down, cover most of the upper and underparts and appear in the tail (fig. 6). Primaries and other wing feathers are by now up to 65 mm. out of their sheaths. At or near the time of fledging the wing measurement (wrist to tip of primaries) of a young bird (fig. 7) was 155 mm. compared to an average of 182 mm. in adults.

Food and feeding of young.—The sand lance (*Ammodytes tobianus*) appears to form almost the exclusive diet of young auklets on Protection Island judging from hundreds of specimens of this small teleost fish dropped by parents entering traps. Only a single specimen of another fish, a smelt (Osmeridae, probably *Hypomesus pretiosus*), was found. Heath (1915) and others have found sand lances to be the only food of Rhinoceros Auklets, but Grinnell (1899) found a small crustacean to be the food of 10 auklets collected in winter off southern California, and Linton (1908) recorded small sardines as the food in several specimens taken off California in late fall. Koslova (1957),

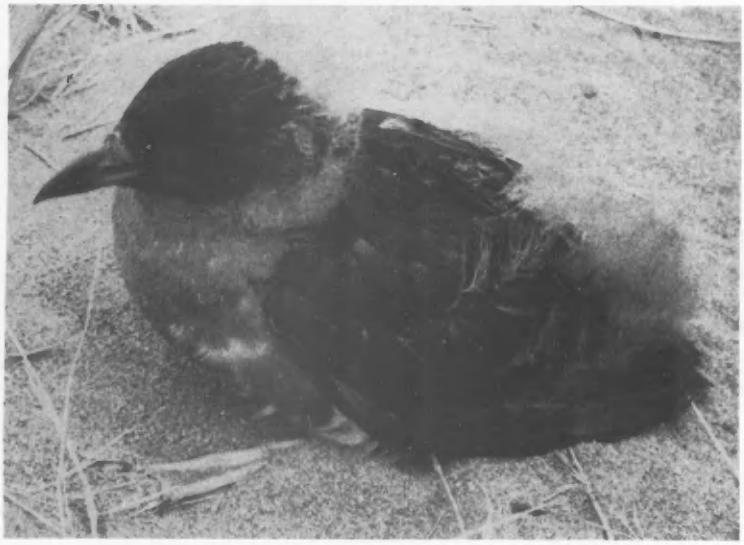

Fig. 7. Young auklet about five weeks old. The young leave their burrows to go to the ocean at about this stage or a few days later even though they are not full-grown. This bird weighed 401 grams compared to an average of 542 grams for adults.

reporting on records from the northwest Pacific, states that Rhinoceros Auklets eat mostly marine invertebrates but that the young are fed two kinds of smelt, young salmon, and other fish.

The number of sand lances carried at one time in the bill of a parent returning to its burrow was often impressive, being as many as 13. In 37 cases the average number of fish brought in was 6.4 with a minimum of one fish on two occasions. The fish were usually between four and six inches long, but occasionally they were as small as two or as large as seven inches. The weights of two billfuls of 10 and 12 fish were 29 and 30 grams, respectively. The ability of the auklets successively to catch and hold a large number of fish in the bill, rivaled by other birds such as White Terns (*Gygis alba*), can be explained by the structure and control of the tongue and bill.

Although the frequency of feeding of young appears to decrease markedly during the week or so before fledging, when the young may gain little or no weight, young are fed nightly or twice nightly before this period. Eighteen records were obtained of two visits to single burrows in one night. In eight cases fish were brought in both times. In two instances catching of banded birds proved that both parents were feeding the young. Two records of three visits to a burrow in a night, and a banded bird returning the same night, show that a parent may make two visits a night presumably to feed the young. In these latter cases, however, trapping could have disrupted the normal feeding schedule.

The regularity of visits to the young is indicated by the fact that of 223 nightly checks of burrows during late June and July, 213, or about 95 per cent, showed that burrows had been entered. Very likely at least a few of the burrows checked were not in use even though appearing to be, so the nightly visitation was even closer to 100 per

cent. However, considering the records in late June and July of burrows with traps in them, 69 of 83 burrows, or about 83 per cent, were entered or visited. Only 60 of the 83 traps, or about 72 per cent, were actually entered, further emphasizing the deterring effect of traps.

Of the 60 times traps were entered and set off, mouthfuls of fish were disgorged 35 times. Apparently parents were entering burrows without food for young in the other 25 instances for I think an auklet's surprise at finding its head in a net, and the push and clatter of the trap door shutting behind it, would always cause it to drop fish.

Observations of traps and burrows appear to show a regular decrease in frequency of feeding but not of visitation after the early growth of the young (table 2). It appears,

TABLE 2

VISITATION OF BURROWS FROM BEFORE HATCHING TO FLEDGING OF YOUNG

Date	Open burrows		Burrows with traps		Mouthfuls of fish dropped
	Checked	Entered	Checked	Entered	
June 1, 1958	33	30	23	8	0
June 18, 1957	50	47	12	10	9
July 4, 1958	34	33	12	10	4
July 13, 1957	64	61	12	7	4
August 1, 1958	29	27	23	11	0

too, that the greatest urge to enter burrows, in spite of the presence of traps, is when the young are small and being fed the most frequently. Fewer birds entered traps on June 1, when incubation was still in progress, or on August 1, when young were nearly fledged, although the visitation of open burrows on these dates was still almost 100 per cent.

The feeding of young does not appear to occur at any definite time during the night. The records for some nights show a preponderance of fish brought in soon after dark but the records for other nights show about equal visitation of the parent birds before or after midnight or more frequent feeding of young in the hour or two before dawn. It was difficult to obtain adequate data on feeding times of young because the auklets were easily disturbed when one walked around the breeding slopes or showed a light.

The need for intensive feeding of the young during their early growth is emphasized by the fact that in late June there are only about six hours (9:15 p.m. to 3:15 a.m.) of darkness each night. The young must thus be adapted to going without food for at least three-quarters of the diurnal cycle. During the later growth, they, like the young of various sea birds such as shearwaters and fulmars, seem adjusted to not eating for a number of days.

The source of the sand lances brought to the young was not determined, but the extreme freshness of the fish, one of which was found still alive, indicated not too distant fishing grounds. Daytime fishing was observed within 10 miles of Protection Island which suggests that the auklets do not go to distant feeding grounds, as to the open ocean some 80 miles away, to obtain food for their young.

Fledging of young.—Apparently all or nearly all the young auklets were fledged by early August. Koslova (1957) indicates a similar date (August 1 to 10) for the appearance of young auklets on the Bay of Taba near Sakhalin Island, northwest of Japan. A number of nearly fledged young, one apparently just taking off, were found in burrows on Protection Island on August 1, 1959, and some fish were being brought in to them. Fewer young were present on this date in 1958 and no fish were known to be brought in. On August 20, 1957, no young were found. The young leave their burrows to fly down

to the water when they still have patches of down and are substantially smaller than adults. Coues (1868) pointed out the marked size difference, particularly of the bill, in fledged young and adults. Koslova (1957) noted young auklets with subadult wing lengths on the water. Limited flight thus appears to develop precociously to enable young to get to the water and undertake a more independent existence. This is in contrast to the Ancient Murrelet (*Synthliboramphus antiquus*) whose few-day-old chicks walk from their shallow burrows to the sea. The behavior of young auklets suggests murres whose half-grown young fly down to the water.

Nocturnal activities of adults.—A consistent relationship to the amount of daylight was shown in the arrival and departure of adults. Auklets started coming to the island about 45 minutes after sunset when it was almost completely dark and when, if clear, numerous stars were out. In the morning, however, the last birds left about 20 minutes before sunrise when it was about half light, or occasionally as on May 3, at 8:15 a.m., in full daylight. Consequently, adults were on the breeding grounds from about 8:00 p.m. to 5:10 a.m. in late March, from 9:15 p.m. to 3:15 a.m. in late June, and from 8:55 p.m. to 4:00 a.m. in early August. These times are approximate since there is no mass arrival or departure of birds. Usually it was 15 minutes or so after the arrival of the first auklets that large numbers started coming in, and the birds continued to arrive in numbers for the next half hour or more. A reverse pattern occurred in the early morning. In either evening or morning there could be so many birds both coming and going during the hour after first arrivals or the hour before last departures that a particular time of arrival or departure could not be designated.

Although auklets started coming in to the slopes at dark throughout the season, usually many more came in after midnight while digging of burrows or incubation were going on than during the weeks when young were being fed. Heavily overcast skies sped the general arrival time or delayed departure for about 15 minutes. No instance of delayed departure of an hour or so due to cloudiness or fog, as cited by Heath (1915), was observed.

Voice.—Dawson and Bowles (1909) speak of the "growls and barks and parrot-like shrieks" of Rhinoceros Auklets on their breeding grounds, but this variety of noises has not been confirmed. Heath (1915:33) describes the call as a "curious nasal cry of four short notes rapidly repeated," which is closer to descriptions of the call in my notes. I recorded the call as consisting of five to seven rather high-pitched, groaning notes with the accent and longest pause usually on the second or third note and the last one to three notes fainter and dying away. At close range a brief, guttural "chuck" was occasionally heard between groan notes. Late in the season a series of three or four low-pitched "chirps," presumably from young, was heard a number of times within burrows.

The calls of different individuals, although similar, showed marked variations in pitch, stress, and number of notes. Perhaps these variations function in helping birds to locate each other in the dark. Call notes were often given from inside burrows and these could help mates locate their burrows. Single, low notes were heard occasionally from inside burrows. Much more calling occurred after midnight, especially during the hour or two before departure of birds at dawn, and this may discount the possible role of calls in locating mates or burrows. In the evening, just before or when auklets were first coming in, and during departure in the morning, auklets were heard many times calling from well out on the water suggesting some gathering of auklets there. A single groan-like call note was occasionally heard, as was a rasping squeak. Vocalizations of Rhinoceros Auklets showed an interesting parallel, both in quality and variety, to those of the nocturnal, burrowing, Wedge-tailed Shearwater (*Puffinus pacificus*).

Mortality.—Two instances were seen of auklets killed by the caving in of burrows by sheep or humans. This cause of death, perhaps serious in some areas, is usually not discovered. Predation appears to be almost negligible as there are no mammal predators and the auklets are not exposed to any diurnal birds of prey. One cleanly picked partial skeleton of an auklet was found which could have been the work of a Horned Owl (*Bubo virginianus*), the only large owl seen occasionally on the island.

Auklets are sometimes killed by flying into obstructions. A wire sheep fence with a 5- to 10-inch mesh ran through the beach grass above the bluff of the study area, and departing auklets were heard to hit it forcefully many times. However, repeated search along this fence revealed only two dead birds which may have been thus killed. This may attest to the strength of the neck and short wings in auklets. Jewett, Taylor, Shaw, and Aldrich (1953) mention auklets being killed fairly often by flying into rocks below breeding slopes when taking off. Numerous searches of the jumble of logs and driftwood below the study area revealed only two dead auklets, so this cause of mortality also seems minor.

Diurnal and postbreeding distribution.—Very few auklets were seen in the daytime in waters near Protection Island, the maximum being 15 seen on July 5, 1948, about a mile out in the channel between the Olympic Peninsula and the island. However, on several occasions from early March to late May hundreds were recorded in Admiralty Inlet about 10 miles eastward from the island, toward Puget Sound. Sufficient data are not available to be sure of the daytime or nighttime distribution of the auklets of Protection Island, but it appears they stay in the more inland water, not going the long distance to the open ocean.

Many auklets continue to return to Protection Island even two or three weeks after the young are fledged. On August 20, 1957, for instance, 63 of 76 burrows had been visited within a few days, and on the night of August 21, 30 of the 76 burrows were entered. No young were found in a number of burrows that had been entered. The few birds caught, none bringing food, were unbanded adults and it could not be determined whether they were nonbreeding or recently breeding birds. Two, probably postbreeding adults, were caught in recently used burrows, but tracks in and out of three uncompleted burrows indicated some indiscriminate entering of burrows at this time. Recently fledged young can hardly be involved, for they are generally many miles from the island at this time and their power of flight is not great. On August 15, 1957, for instance, at least 200 adult and young auklets, presumably from Protection Island as it is the only breeding grounds in the whole region, were seen in the channel east of San Juan Island, some 25 miles to the north. These birds could not be made to fly when repeatedly approached by boat.

In early September of two years no auklets were returning to Protection Island. A few are present each year in the Puget Sound region from September to February but these may be migrants from the north. A maximum of 24 of these wintering auklets was seen off the west side of Bainbridge Island on February 2, 1958. Apparently nearly all auklets go to the open seas or coast during the winter. Some migrate as far south as Baja California.

BEHAVIOR

A somewhat miscellaneous group of observations is included in this section. Although related to the breeding activity in varying degree, they do not fall under the major headings discussed there.

Flight.—Auklets hurtle directly toward Protection Island at high speed and with rapid wing beats regardless of darkness. Normally they sweep somewhat upward on the

slopes before alighting, a fact that would seem to make low burrow sites less desirable. Although some observers have commented on auklets frequently landing with a crash, as in vegetation, I found they almost always landed rather lightly after a forceful flutter of wings. Occasionally auklets struck the ground rather hard or landed in the beach grass with much rustling, but these seemed to be atypical examples of poor judgment or poor visibility.

Fairly often, especially when first coming in after dusk, one or more auklets would swerve across the face of the slopes for a distance and head back out to sea. Birds thus seemed to determine that darkness was not yet complete enough for their safety on the ground, although their behavior may have been analogous to the "passing flights" often seen in Tufted Puffins.

Rhinoceros Auklets, perhaps especially the fledgling young, must launch themselves from a slope or bank when taking off from land. Auklets could not take flight from the deep beach grass or from burrows about 10 feet above the beach. Birds liberated at night generally took off very quickly but those liberated in the daytime often ran to escape. One, curiously, repeatedly swam back to shore when liberated into the water. Capture and subsequent liberation clearly disturbed the auklets. Instincts to run away or find shelter on or under the ground seemed to conflict with flight movements.

Relation to burrows.—The highly developed fossorial habits of Rhinoceros Auklets are shown not only by their extensive digging and entering of breeding and accessory burrows both during and after the breeding season but also by the frequent attempts of both young and adults to escape into burrows when liberated. In one case an adult, liberated at night next to its destroyed burrow, quickly ran into another burrow about four feet away.

Auklets, although showing a high degree of specificity to their burrows, were several times noted to adopt new entrances where cave-ins destroyed the outer one to three feet of burrows. Several double entrances, never more than a foot or so apart, were seen. They appeared to result from excavation or small cave-ins, and only one entrance was regularly used. Although burrow entrances of separate pairs of birds were sometimes only 6 to 12 inches apart, in only one case were two pairs found to use a common entrance, the burrow then branching immediately into right and left passages.

Accessory burrows seemed usually to be manifestations of digging proclivities but one such burrow, not used for breeding, was about two feet deep and had feathers and nest material in it, suggesting it might be a dummy nest. In June and July of 1958, four burrows used for breeding in 1957 were found to have been entered numerous times even though they were not being used for breeding purposes. The opening and covering of these burrows from the back may have led to their desertion in 1958 although they were not deserted in 1957 when eggs and young were present.

Incubating adults would rarely leave their burrows when I attempted to dig them out in the daytime, but in one instance a bird came out when I was digging about four feet from its nest. Five incubating birds, taken by excavation from the backs of burrows, all returned quickly to their burrows and did not come out during the day. These and other observations indicate the auklet's aversion to being in the open on their breeding grounds in daylight.

Temperament.—Rhinoceros Auklets display a vicious temperament when captured and use the strong bill and sharp claws violently and effectively in efforts to escape. This temperament is slow to manifest itself in the young, but nearly fledged birds five weeks old were very aggressive although they could never have seen a human before. Adults when caught in traps or handled did not give any vocal notes except an occasional grunt

caused perhaps when they were tightly held. A nearly fledged young, however, sounded a high-pitched note when caught by hand.

Activities on slopes.—Nightly, during the whole breeding season, there were many auklets walking, running, or standing on the slopes. Many of the birds seemed to have no purposeful activity for they often stood in the same spot, not adjacent to burrows, for 20 or more minutes at a time. Others walked around, rather aimlessly it appeared, or more often ran, the body typically held nearly parallel to the ground and the neck low and outstretched. The birds thus seem to scoot low to the ground, a pose which must be approximated as they go through their burrows (fig. 8).

Fig. 8. Auklet resting in beach grass above bluff at night. The squat stance, resting on the tarsometatarsi, is typical. The head and neck are lowered when the bird runs.

My notes for 2:30 to 3:00 a.m. on July 4, 1958, give some further indication of auklet activities: "Some 10 birds were seen at one time from the blind, all from 6 to 30 feet away. Birds intermingled without altercations. Two or three pairs were seen standing together but others were single, or three or more were together." Standing birds at night were several times seen to stretch and flutter their wings, perhaps drying their feathers.

There do not seem to be recognized territories around burrows and we can perhaps best think of the burrows themselves as constituting the territory of each pair of auklets. The very distribution of the burrows, ranging from close together to widely scattered, suggests that Rhinoceros Auklets are not a truly colonial breeding bird beyond the point of showing a selectivity for certain islands. On Protection Island their distribution is largely due to the suitability of slopes or soil; the frequently widely-scattered pairs of auklets show no attempt to congregate into a close-knit breeding colony.

SUMMARY

A portion of the long-established breeding grounds of the Rhinoceros Auklet on Protection Island, Washington, was studied on monthly trips in the course of four breeding

seasons. Seventy-six burrows were marked and followed; a total of 71 auklets were banded.

The return to the island of the population of an estimated 3000 to 4000 pairs of adult auklets starts in early March but is not complete until late in the month. The digging of burrows or reclamation of old ones begins at once.

Preferred burrowing sites are generally in firm, sandy soil on slopes of between 37° and 45° or in dense growths of beach grass (*Ammophila*) above steep slopes.

Both members of a pair of auklets excavate their burrow, using the bill and claws in digging. The rate of excavation averaged 7.6 inches a night.

Banding returns indicate that auklets typically maintain the same pairs each year and use the same burrows.

No consistent colonial or territorial behavior is exhibited and burrows may be from one to dozens of feet apart. The study area of about one-third of an acre contained about 132 active burrows.

The single eggs are laid as early as April 21 or as late as May 30 but generally about mid-May. Incubation is performed by both parents and apparently the young hatch in 31 days plus a day or two. No evidence was found of a regular evening and morning exchange of incubating birds, but most burrows are entered each night.

Temperature control is established in the young, densely down-covered auklets within a day or two after hatching. Correlated with this and the uniform, mild temperature of the burrows, the young are apparently not brooded.

The sand lance, *Ammodytes tobianus*, appears to form almost the exclusive diet of the young auklets in this study area. A parent may bring in as many as 13 of these four-to-six inch fish at once in its bill. Both parents bring fish to the young auklet, feeding taking place nightly at least during the early weeks of growth of the young.

Growth of the young from hatching to fledging takes approximately five to six weeks, but the fledgling is definitely of subadult size and just able to fly down to the water from its burrow. All young auklets are fledged and gone from the island by early August, but numerous adults continue to return to the breeding grounds at night until late August.

Whether in March or July, the auklets start coming to the breeding grounds about 45 minutes after sunset. There is much coming and going during the night, but virtually all auklets leave the island by 20 minutes before sunrise. Rain or overcast skies do not appear to change these limits by more than 15 minutes.

The chief cause of mortality of auklets on Protection Island appears to be the caving in, or burying through earth slides, of burrows by sheep or people. The denuding by sheep of slopes used by breeding auklets is seriously decreasing suitable nesting areas.

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TIMING OF ANNUAL MOLT IN THE GLAUCOUS GULLS OF NORTHERN ALASKA

By David W. Johnston

In northern Alaska there are many adaptations for the successful existence of birds and mammals in a cold climate. Important among these adaptations are those of both anatomical and physiological natures. Some of these have been discussed recently by Irving (1960).

The majority of the birds breeding under these northern climatic conditions encounter an abbreviated season for the important processes of reproduction and molt. It is well known, for example, that many of the small passerine and shorebird species arrive in arctic Alaska about the first of June and depart for the south at least by mid-August. In this brief period they complete the entire breeding process and begin, or even complete, the annual or postnuptial molt. These two major events are therefore condensed into a shorter period than would be the case in warmer latitudes. In larger species, such as the Common Raven (*Corvus corax*) and Glaucous Gull (*Larus hyperboreus*), there are two additional problems: the incubation periods are longer, and the large flight feathers require more time for replacement. The present investigation will discuss these features of the Glaucous Gull as they pertain to the arctic breeding period.

During the summer of 1960 I was a consultant for the United States Public Health Service, along with several other ornithologists, to study the bird life of the arctic coast of Alaska in the vicinity of Cape Thompson (latitude 68° 06′N, longitude 165° 46′W). These investigations were supported by the Division of Biology and Medicine of the Atomic Energy Commission (Agreement No. SF–54–373, environmental studies of Project Chariot). Since our work dealt mainly with populations of small passerine species in terrestrial communities, the observations reported here were incidental to our major duties, a detailed account of which will appear later. My colleagues, John Q. Hines, Max C. Thompson, Francis S. L. Williamson, and Jerry Tash, gave valuable assistance in collecting specimens, and Leonard Belson and George W. Cox have provided a few unpublished breeding data from the cliff-nesting population. Special acknowledgments are due Francis S. L. Williamson for his pertinent suggestions in the preparation of this paper.

OBSERVATIONS

In the Cape Thompson region, Glaucous Gulls appear in the spring toward the latter part of April or early May, their appearance and numbers depending largely upon the melting of the sea ice. Upon my arrival at Cape Thompson on May 30, I immediately noticed to my surprise that *all* the Glaucous Gulls flying along the shore were symmetrically replacing their primaries. This fact assumed greater significance when it was realized that this species had either just begun to incubate or had not yet laid any eggs. At best, these observations suggested that the local Glaucous Gulls had begun their annual molt before or soon after incubation had begun, a rather unusual phenomenon among birds. In order to determine the validity of such an interpretation, I decided to take at random occasional samples of adult gulls throughout the summer months and to learn, within the limitations of time, as much as possible about the local breeding population in relation to molt. No specimens were taken directly from the nest sites but rather from the nearby ocean shores where no doubt individuals from the cliffs and lagoons foraged together.

As the result of previous investigations by a team of workers from the University of Alaska, it was already known that there existed on the sea cliffs at Cape Thompson a

small, scattered colony of nesting Glaucous Gulls along with thousands of murres and other species. In 1960, the first nests with eggs were discovered on June 6, but presumably some of the eggs had already been incubated for about two weeks. Although the first young gulls were seen at these cliff nests on June 16, other nests still containing eggs were in evidence as late as June 30. If the incubation period for this species in northern Alaska is 28 days (see Bent, 1947:55; Witherby, *et al.*, 1941:109), some eggs in the colony were probably laid as early as May 19 and some as late as June 2. Furthermore, two adult females, taken June 5 and June 11, still had collapsed follicles in evidence, indicating that egg laying had occurred recently.

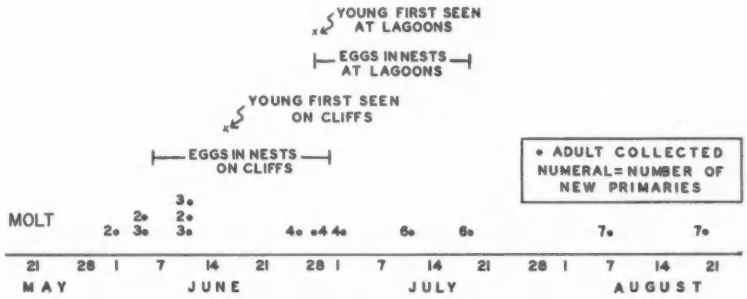
YOUNG FIRST SEEN AT LAGOONS
EGGS IN NESTS AT LAGOONS
YOUNG FIRST SEEN ON CLIFFS
EGGS IN NESTS ON CLIFFS
• ADULT COLLECTED
NUMERAL = NUMBER OF NEW PRIMARIES
MOLT
2• 2• 3• 3• 2• 3• 4• •4 4• 6• 6• 7• 7•
21 28 1 7 14 21 28 1 7 14 21 28 1 7 14 21
MAY JUNE JULY AUGUST

Fig. 1. Sequence of selected reproductive stages and primary molt in adult Glaucous Gulls at Cape Thompson, Alaska.

In addition to Glaucous Gulls nesting on cliffs, we located many scattered pairs nesting at the edges of lagoons both north and south of the Cape Thompson cliffs. Most of these lagoon-nesting pairs were near the mouth of the Kukpuk River or in the Point Hope area, up to fifteen miles northwest of the cliffs. Other nests were discovered about twenty-five miles southeast of the cliffs near the mouth of the Singoalik River, and we suspected that the gulls were breeding around some of the larger lakes inland from the cliffs. Unfortunately these lagoon sites were not always readily accessible except by occasional airplane visits, so less detailed observations were made there. Nonetheless, the first young gulls at lagoons were seen on June 28, at which time some nests still contained eggs. Eggs were seen in nests as late as July 19. The first possible date for egg laying would have been about June 1. It is of passing interest to note here that the cliff-nesting Glaucous Gulls in general nested earlier than the lagoon-nesting ones, but this was to be expected since the cliffs are free of snow and ice before the lagoons.

Figure 1 summarizes these events in the nesting cycle for this species in the Cape Thompson region. Included also in the figure are the dates when adult specimens were taken and the extent of each bird's primary molt. Although details of body molt were not studied extensively, it was evident that the specimens taken as early as June 1 and 5 were beginning to molt flank feathers. Body molt did not become extensive, however, until the end of June. From that time through August 19, body molt was "heavy."

The departure of Glaucous Gulls from the Cape Thompson region appears to be rather leisurely and is dependent, at least in part, on the reappearance of the sea ice. According to the observations of Max Thompson, many were still present along this stretch of the coast as late as November 10.

DISCUSSION

The breeding cycle of the population of Glaucous Gulls at Cape Thompson seems to differ little from that of other populations in Alaska. Grinnell (1900:10) noted arrival of this species at Kotzebue on May 11. Bent (1947:61) stated that eggs were laid in northern Alaska between May 26 and June 28, whereas Kessel and Cade (1958:59) reported birds at Umiat between June 4 and September 8, with young hatching at the Colville River delta as early as July 6. Glaucous Gulls leave Point Barrow about November 1 (Bent, 1947:61). The breeding season in Spitsbergen is reported by Witherby, *et al.* (1941:109) to extend "from end May to mid-June." It would appear from these reports and from the data presented in this paper that the Glaucous Gull is a relatively early nester in the Arctic.

Few precise data are available for the annual molt. Dwight (1925:94) remarked that for any large gull with a four-year plumage cycle in the northern hemisphere, "postnuptial molt is mid-July to the end of September," and for *hyperboreus* he stated that there is a complete postnuptial molt in August and September. Johnston (1955:204) noted that four adults taken at St. Michael on June 7 were molting primaries. On Nunivak Island, Swarth (1934:36) reported: "September adults are molting, and two specimens collected on October 8 are the only ones in which molt of the remiges had advanced as far as the replacement of the outermost primaries, which in these birds are partly grown." Clearly, however, the Glaucous Gulls of the Cape Thompson region had already replaced two of their primaries by June 1. In this species the precise rate of replacement and growth of the primaries is not known, but from the specimen data presented in figure 1 it is probable that the first (smallest) pair of primaries required about ten days for replacement and the larger ones about thirteen or fourteen days each. If this were true, it would mean that molt of the first primary occurred about May 11. Considering then the molt data and the evidence for time of egg laying, it seems obvious that this species begins its annual molt of primaries either before the first eggs are laid or certainly immediately thereafter.

Many instances could be cited for species of the temperate zone which effect their annual molt after their eggs are hatched or after the young have left the nest, this sequence being the rule for many of the other species breeding in the Cape Thompson region. Even in the Black-legged Kittiwake (*Rissa tridactyla*), the other common breeding larid of the Cape Thompson region, adults procured in late July and early August when they had young in the nest had not yet begun the annual molt of primaries. Kittiwakes are apparently late nesters elsewhere in Alaska (Gabrielson and Lincoln, 1959: 457) and in England (Witherby, *et al.*, 1941:116). By way of contrast, the California Gull (*Larus californicus*), breeding in California, lays its eggs by May 11, with the adults molting their primaries from mid-June (after the eggs hatched) until September 1 (Johnston, 1956:140).

Various authors have related the timing or inception of the annual molt to such factors as photoperiod, amount of food, or changes in temperature (Pitelka, 1958; Lesher and Kendeigh, 1941:169). In the Glaucous Gull, the beginning of this molt and its duration are related especially to size of the bird and the available time for breeding. In other words, since the breeding season is relatively short in the Arctic and since much time is required for the molt of the large primaries, these two events are telescoped so that they overlap broadly. The early beginning of the molt allows this species to complete its molt and reproduction on the breeding grounds. Since this species evidently does not suffer from a dearth of food even in late autumn and since it does not migrate especially early from arctic Alaska, it seems unlikely that this early molt has any present

adaptive value. Nevertheless, there are several speculations which seem to be appropriate. The early molt could have originated at a time when it was adaptive. Or, it could be adaptive now on an overall basis in the event of occasional early inclement weather conditions in the fall. It would seem beneficial to the species if the energy-demanding process of molt could be consummated before migration.

A final point relating to the timing of breeding in the Glaucous Gull is worthy of mention. Gabrielson and Lincoln (1959:458) state that "farther north the place of the Glaucous-winged Gull is taken by the Glaucous Gull" as chief predator on the eggs and young of the kittiwake. In the Cape Thompson region, however, a cursory study of predator-prey relationships of the sea birds indicated that this large gull was more omnivorous than the foregoing statement would imply. It preyed upon the abundant murre eggs and, more so, was a conspicuous scavenger of murre, puffin, and aquatic mammal carcasses. In fact, throughout the summer we could almost always find a group of these large gulls feeding on walrus and whale carcasses, some of which had been lying on the beach for at least a year. One might be tempted to suggest that the nestings of the Glaucous Gull are timed in such a fashion as to have readily available food for their own young (the nest contents of kittiwakes and murres). But such a hypothesis is untenable when the ready availability of other food items is considered carefully.

SUMMARY

In the Cape Thompson region of arctic Alaska, the Glaucous Gull (*Larus hyperboreus*) lays its eggs in late May or early June. Adults begin their annual molt before or soon after the eggs are laid, that is, by the end of May. This early molt is believed to be an adaptation whereby this species is able to complete, or nearly complete, both breeding and molt during the abbreviated summer period.

Glaucous Gulls were found nesting in two distinct habitats: (1) on precipitous sea cliffs and (2) on small islands or peninsulas or at the edge of lagoons and lakes. The cliff-inhabiting individuals bred before those at the lagoons.

The timing of nesting is not necessarily related to an abundant supply of eggs and/or young of kittiwakes since other food items are readily available throughout the summer.

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A STUDY OF NESTING ANT-TANAGERS IN BRITISH HONDURAS

By Edwin Willis

From the middle of February to early in August, 1957, I studied Red-crowned and Red-throated ant-tanagers (*Habia rubica* and *Habia gutturalis*) at Gallon Jug, British Honduras. Earlier articles have described voice and courtship behavior (Willis, 1960*a*) and foraging habits (Willis, 1960*b* and 1960*c*). Here nesting will be considered.

Thanks are due the National Science Foundation for two fellowships supporting this study, the United Fruit Company for transportation to Belize, British Honduras, and the Belize Estates and Produce Company and the many generous people of that organization for their assistance in many ways at their camp at Gallon Jug. A. F. Skutch has volunteered several suggestions; R. J. Newman, of the Museum of Zoology at Louisiana State University, has examined the manuscript critically; and G. H. Lowery, Jr., directed the study.

BREEDING SEASON

About a dozen closely-observed pairs of ant-tanagers began nesting in late March in the dry season and continued through June and July, the first and wettest months of the rainy season. The distribution of 22 nests of Red-crowns according to the quarter-month when a clutch was completed was: April—1, 2, 2, 1; May—1, 1, 2, 0; June—2, 1, 1, 2; and July—2, 3, 1, 0. The distribution for nests of Red-throats was: May—2, 1, 3, 3; June—5, 5, 2, 3; and July—2, 1, 1, 0. During the last half of July, I stopped searching for nests, so that ant-tanagers may have nested more commonly at that time than my records indicate. Other ornithologists have reported nests of ant-tanagers elsewhere in Central America as early as late March and as late as August. Since ant-tanagers utter dawn songs mainly while nesting, dates of breeding can be approximately determined by listening for such songs.

SEARCHES FOR NEST SITES

On eight occasions I saw pairs of Red-crowns that were looking for nest sites. The female did the most active searching. Chattering frequently, she sat in one crotch after another in saplings or forks of limbs. At times the male flew to a limb near her and called; less often he spread his tail or wings as well. After the female chattered and flew away, he sat down at the same spot and pecked at the air in the same fashion as she had, seemingly moving strands of nesting material. He usually gave only faint *chook* notes and day songs except when investigating a site. Then he chattered as volubly as the female. On only one occasion, March 30, did a female carry fine strands to several sites as she searched.

LOCATION OF THE NEST

Generally nests of ant-tanagers were set against the stems of saplings on small branches or on the petioles of large leaves, although four nests of Red-crowns were on the forks of branchlets up to half a meter from the trunks. A few Red-crowns built above the crotches of saplings in such a way that the nests were supported only by vertical branches. But the loose and leafy nests of Red-throats were supported at the bottom by twigs, vines, or petioles.

Many nests (table 1) were in wild coffee (*Rinorea guatemalensis*), the most abundant sapling of the forest at Gallon Jug. Twigs of wild coffee commonly spread in whorls of six or so from the stem and provided excellent supports for nests. *Piper psilorhachis* or Spanish elder, the next most common sapling, and *Pouteria Meyeri* or fever grip, the

TABLE 1

SITES OF NESTS OF ANT-TANAGERS

Plant[1]	Number of nests of Red-crowns	Number of nests of Red-throats
Rinorea guatemalensis	7	17
Piper psilorhachis	5	1
Pouteria Meyeri	5	1
Bactris mexicana	0	3
Cryosophila argentea	0	2
Cupania guatemalensis	0	2
Psychotria grandis	2	0
Bursera simaruba	1	0
Pseudolmedia sp.	1	0
Manilkara zapotilla	1	0
Chamaedorea concolor	1	0
Pouteria Durlandii	0	1
Ouratea Peckii	0	1
Aspidosperma megalocarpon	0	1
Terminalia sp.	0	1
Coccoloba sp.	0	1
Unknowns 1, 2, 3	1	2

[1] Specimens from Gallon Jug were compared by the author with specimens in the United States National Herbarium.

third most common, were less often used by Red-throats than by Red-crowns. Spanish elder and fever grip branch sparsely and offer few places with both the bottom and the side supports necessary for nests of Red-throats. Palms were rarely used by Red-crowns; a nest in a *Chamaedorea concolor* eventually tilted and tumbled the young bird to the ground. Two nests of Red-throats were set in the most common palm of the undergrowth, the spiny give-and-take (*Cryosophila argentea*); one nest was placed atop two leaves. Three nests were in the wickedly spined *Bactris mexicana*, set on petioles and secured by the proximal two or three pairs of leaflets. The theory of Peck (1910) that the spininess of such palms discourages predators was not confirmed by the fate of these three nests, for all the eggs were stolen soon after they were laid.

Nests of Red-throats were generally lower than those of Red-crowns, in keeping with the lower foraging zone of the former species (Willis, 1960*b*). The highest nest of Red-crowns was 5.7 meters up, the highest nest of Red-throats only 3.7 meters up. The saplings used were from 1.4 to 7.0 meters high, and most of the nests were situated five- to nine-tenths of the way up. However, one nest of Red-throats in a *Bactris mexicana* was only about one-fourth of the way up the leafy cane.

Few nests were placed among crowded twigs and none in dense leaves, perhaps because the birds had some difficulty flying through thick growth and avoided dense tangles most of the time. Before one male Red-throat found a way in to his nestlings, he was turned away on two attempts by the barricade of twigs in which his mate had built the nest. However, shade and concealment were often provided by fallen dead leaves or attached green leaves a few centimeters above nests.

Ant-tanagers nearly always used sites with relatively clear views in one or more directions. Several nests were placed alongside paths or bulldozer trails. Possibly such advantages of exposed positions as the presence of better vantage points and of unobstructed routes for escape outweighed any disadvantage of greater conspicuousness.

The nests were usually in high forest. No nest of Red-crowns was in high second

growth, although some second growth was 15 meters in height and was used in foraging. One nest of Red-crowns, from which the eggs were soon stolen, was placed at the border of a small, recently-cleared cornfield; another was at the edge of low second growth. The latter site was used later in the season by a female Red-throat for her nest; neither nest was successful. Two out of 33 nests of Red-throats were in high second growth, and a third nest was about 10 meters out from the edge of the forest, in shrubby growth less than a year old. Set on a leaf of a sprout of *Coccoloba* sp., this nest was soon torn down by a predator.

The nests of each pair were built within the foraging area and territory of that pair. On a few occasions nests were built near each other. The fourth nest of one pair of Red-throats was built 30 meters northeast of the second nest of another pair while the female of the latter pair was incubating. Two pairs of Red-crowns had occupied nests 120 meters apart in July, whereas the two mates of one male had nests about the same distance apart in July. In May I watched a nest of Red-throats out the front of a blind and kept an eye on a nest of Red-crowns out the left side of the blind; the two nests were about 15 meters apart.

NEST MATERIALS

For birds so alike in appearance as are the species of ant-tanagers, the materials used by the two species (table 2) and the final appearance of their nests (fig. 1) were surprisingly different. The nests of Red-crowned Ant-Tanagers were neat, shallow cups made of slender epiphyte rootlets, rhizomorphs, and plant fibers, and they were so thin that the eggs were sometimes visible in silhouette from underneath. In contrast, nests of Red-throated Ant-Tanagers were loose cups constructed of leaves, vines, and other bulky

TABLE 2

MATERIALS USED IN NESTS OF ANT-TANAGERS

Species:	Red-throats								Red-crowns			
Nest:	1		2		3		4		5		6	
Body or Lining:	B	L	B	L	B	L	B	L	B	L	B	L
MATERIAL:												
COARSE												
Dead leaves	47	—	13	—	19	—	29	—	2	—	—	—
Palm fragments	9	1	39	—	39	—	33	2	—	—	—	—
Fern pinnae	3	—	—	—	—	—	—	—	—	—	—	—
Moss strip	—	—	—	—	—	1	1	—	—	—	—	—
Thin strips of bark*	9	—	13	3	—	—	1	1	—	—	—	—
Winged seed	—	—	1	—	—	—	—	—	—	—	—	—
Twiglets (2 mm. diam.)	4	—	2	—	—	—	—	—	8	—	1	1
Leaves or twiglets whitened by fungus	3	—	7	—	10	—	—	—	—	—	—	—
MEDIUM (0.5–1.5 mm. diam.)												
Stems of herbs	—	—	3	1	1	1	2	—	5	—	—	—
Vinelets, tendrils, and rootlets of epiphytes	38	—	42	—	27	9	19	5	139	—	165	2
FINE												
Fibers from stems of herbaceous plants	2	—	—	2	—	—	1	—	32	—	—	—
Rhizomorphs	--	61	—	59	—	38	—	37	19	80	14	50
Spider webs	+	—	+	—	+	—	+	—	+	—	+	—
Total of pieces:	115	62	120	65	96	49	86	45	205	80	180	53

Notes: * mostly fragments of bark from saplings of *Bursera simaruba*; + means that material was present, — that it was absent.

material. Such bulky nests resembled the piles of leaves and debris that collected in bushes here and there in the forests at Gallon Jug. Both species lined nests with rhizomorphs or "vegetable horsehairs," the fungal hyphae of *Marasmius*.

In external dimensions, 16 nests of Red-throats averaged 10.7 cm. (standard deviation [s.d.] 0.50 cm.) in width by 6.4 cm. in height (s.d.=1.33 cm.); 11 nests of Red-crowns averaged 9.2 (s.d.=0.26) by 5.5 (s.d.=0.32) cm. in width and height, respectively. The conspicuous white fungus-covered twigs and midribs of leaves (for a photograph of such "decorations" on the nests of other tropical species, see Sick, 1957) on nests of Red-throats, and the few pendent leaves on the nests of both species, often pro-

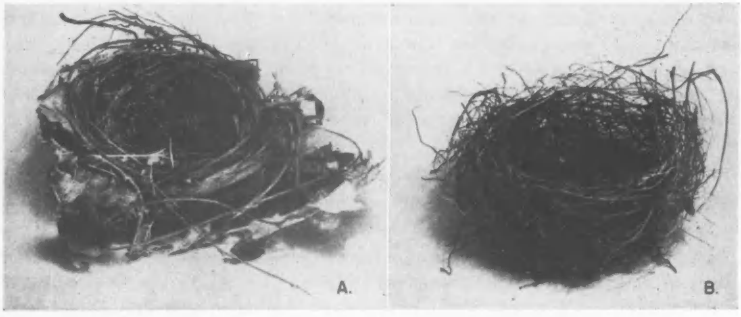

Fig. 1. Nests of ant-tanagers. A, Red-throated Ant-Tanager; B, Red-crowned Ant-Tanager.

jected beyond the nest itself. The inner cups of the same nests averaged 6.7 cm. across by 3.6 cm. deep for Red-throats and 6.1 by 3.0 cm. for Red-crowns. The respective standard deviations are: 0.25; 0.19; 0.18; and 0.19. Female Red-throats average slightly larger in size than female Red-crowns (Willis, 1960*b*), which may explain the larger size of the nest cup in Red-throats.

THE SEARCH FOR MATERIAL

Once I saw a male Red-crown sit briefly on a nest and move strands with his bill. On three other occasions he and another male carried fine strands toward their nests as they followed their mates, but both males dropped their material and darted off with their mates when the latter finished working on the nests. Male Red-throats were never seen to carry material.

Males of both species uttered day songs softly as they followed their busy mates to and from the nests. Occasionally a male inspected the nest before he followed his mate away. Although females searching for material were quiet and scarcely seemed to notice me, their mates were more noisy and evident than usual, and frequently the latter distracted my attention or gave loud notes that caused the females to dart behind the foliage. At other times males drifted off and females visited their nests alone.

The other birds of each family of ant-tanagers were generally less attentive than were adult males, although immature (or adult female) Red-throats often followed nest-building females. Such a group of Red-throats hurrying toward the nest through the undergrowth, the female trailing a long strip of a palm leaf from her bill and crooning a rapid series of faint notes as the male and others followed, was a rather amusing sight. At stops, where all looked around, the immature or immatures foraged briefly as the adult male uttered a few faint songs; then all darted off in the wake of the crooning

female. Immature Red-crowns were less active, and they followed the back-and-forth movements of pairs imprecisely. Female Red-crowns never uttered crooning notes at such times.

At least one nonbreeding bird in one family of Red-throats carried material to and worked on a nest that the female was building. Skutch (1935) has recorded similar "helpers at the nest" for a number of other tropical species.

When a female Red-crown hunted for material, she often visited places where a tangle of branches and vines had fallen to the ground. There she pecked busily at the bark of rotten limbs, pulling and fluttering until the rhizomorph or anchoring root of bromeliad or orchid epiphyte snapped off. Females seldom investigated living trunks and branches, perhaps because rootlets of epiphytes were difficult to remove from live bark. But at times a female went to high limbs and gathered such material as the spider webs used in binding nests to twigs.

Female Red-throats obtained material in similar sites and in several other locations as well. For strips of fronds and fragments of crowns, they visited the tops of various palms. They jerked brown or skeletonized leaves from their mycelial attachments in piles of leaves above the ground and snapped off the birchlike fragments of the bark of gumbolimbo (*Bursera simaruba*) in the fashion of flycatchers capturing insects. Females fluttered and clung to tree trunks, tugging actively, to obtain dead stems and tendrils of small vines to bind the nest. The conspicuous white fungus-covered decorations for the nest were obtained from the litter on the ground or from places just above the ground.

One female Red-throat returned again and again to an area 230 to 270 meters from her nest. Ordinarily searches radiated out 50 to 100 meters from the nest and seldom ended closer than 20 meters. Red-crowns looked for material at similar distances. One female returned repeatedly to an area 130 meters from her nest.

CONSTRUCTION OF THE NEST

The interval between the start of building and the laying of the first egg averaged about a week for ten nests of Red-crowns and about six days for fifteen nests of Red-throats. No new material was added to some nests during a period of as much as a week before the eggs were laid; indeed, building was very slow on the fourth and later mornings of nest construction. Periods of about four or five days between the start of nest building and the laying of the first egg, an interval about normal for tanagers in Central America (Skutch, 1954), were definitely noted in a few repeat nestings. The last egg of one pair of Red-throats was destroyed on May 22, and the first egg was laid in a new nest on May 28. The female of another pair, the eggs of which were destroyed June 2, had laid the first egg in a new nest on June 7. A male Red-crown whose first mate was killed by a Ferruginous Owl (*Glaucidium brasilianum*) had a new mate by the next noon. A new nest was under construction on the following morning, and the female laid an egg four days later.

By placing leaves in some nests for the females to throw out or press down if they returned, and by watching during the afternoon at a few other nests, I determined that few visits were made to nests of ant-tanagers in the afternoon. Except for one visit to the nest in the evening by each species, extreme times for visits were 5:15 a.m. and 10:45 a.m. for Red-throats and 6:04 a.m. and 2:19 p.m. for Red-crowns (fig. 2).

Females differed from each other in their hours of greatest activity and from day to day. Typical hourly records of visits for two female Red-crowns, each on the second and busiest day of nest construction, are 2—2—8—15—8—0 (observed from 6:13 a.m. to noon), and 13—14—7—9—2—4—0 (from 6:00 a.m. to 12:30 p.m.). Similar records

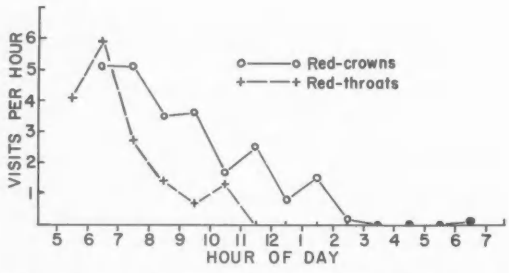

Fig. 2. Diurnal pattern of nest building activity of ant-tanagers.

for two nests of Red-throats on the second or third mornings of nest construction are 0—5—2—3—3—2—0—0 (from 5:50 a.m. to 12:35 p.m.) and 15—4—0—1—1 (from 6:11 a.m. to 11:00 a.m.).

When approaching their nests, female ant-tanagers generally stopped about ten meters away, looked around, and then darted quietly to the edge of the nest. Sometimes female Red-crowns stopped several times closer to the nests, and occasionally hopped up or down to the nests from stops on the nest saplings. Although female Red-crowns might chatter softly as if in answer to the warblings of their mates a few meters away, they were rarely noisy at the nests. Female Red-throats called *sotto voce* at times, but their notes usually were drowned out by the day singing and scolding of the males ten meters or so from the nests.

If I passed while a female Red-throat was on her nest, she froze while the male and other members of the family foraged near me. If I entered the blind, the female resumed slow and quiet activity after a few minutes and finally darted away silently. Female Red-crowns were more likely to dart away while the males chattered near me. If I approached at the same time as did a pair of Red-crowns or Red-throats, the birds flew around and called vigorously until I entered a blind or watched the nest from some distance; then the female slipped cautiously on the nest while the male foraged near me.

Just before the female Red-crown sat down on her nest she placed any material she was carrying beneath her. When the nest still consisted of only a few strands and spider webs looped around some of the supports, she frequently used her bill in pulling a strand from underneath her up over other material or over the nest supports. Then she tucked the strand in on the other side of the material or the support of the nest, thus securing the nest. By the time the female added the first layer of epiphyte rootlets, the nest was a thin disk or cup, depending on the presence or absence of supports underneath. At this stage the female shaped the nest with vigorous movements of her feet. The female sat low on the nest while working and rarely stood up. As she pressed her body down into the forming cup of the nest, she paddled her feet rapidly back and forth. Often her wings and tail were spread out and down with the vigor of her pressing; as she stopped moving her feet, she bounced back up to a sitting or half-standing position, and her tailed closed and rose to some ten or twenty degrees above the horizontal. One female I watched always lifted her yellow crest as she half rose from this pressing and paddling movement. Each female repeated pressing and paddling as many as fifteen times during a visit, turning through a slight angle and tucking loose ends of strands into the nest with her bill. Using her bill, she often arranged the longer strands in a circle around the inside of the nest before rapid movements of her feet matted them into the rest of the

material. Soon the sides of the nest were so thick that the movements of the feet were concealed. During the final stages of building, the material was often deposited on the edge of the nest or on adjacent twigs or leaves before the female settled in the nest. The lining was added with little use of the bill but with much pressing and paddling once she had moved the strands underneath her.

Female Red-throats worked in similar fashion, but they were more energetic than Red-crowns, which worked with finer material. Often the slender sapling quivered with the movements of a female Red-throat. Little use of the bill was required to wind vinelets or spider webs around supports, since nests of Red-throats had supports underneath; but females tucked in loose vinelets or rhizomorphs with their bills. When a female Red-throat brought a leaf to the nest, she occasionally stayed on the nest as little as 20 seconds. When I disturbed one female, she stayed on the nest 30 minutes. The average time for 60 undisturbed visits was one and three-quarters minutes. The interval between visits, although usually over two minutes, was as little as 25 and 30 seconds at a nest where another bird of the family may have been helping the female.

On a few occasions, female Red-crowns merely dropped material and left after a visit of as little as 10 or 20 seconds, although the average for 159 visits was one and three-quarters minutes. Once, when a female stayed on the nest for 11 minutes and 25 seconds, she sat as if incubating. The interval between visits was seldom less than a minute, although I have records of intervals as short as 20 and 25 seconds.

When she departed from the nest, a female Red-crown usually looked around briefly, dropped from the nest, and darted past her mate with a *chauf chauf* or a faint chatter. The pair then moved rapidly away from perch to perch. A female Red-throat usually darted away silently, although chatters drifted back to me from a distance at times.

EGGS

One out of 21 sets of Red-throats was of four eggs, and two were of two eggs; three out of 16 sets of Red-crowns were of two eggs. Other sets consisted of three eggs each. The eggs were laid about dawn on successive mornings. The following description from my notes would serve equally well for either Red-crowns or Red-throats in illustrating behavior connected with laying: "*April 18* (sunrise, 5:42 am)—Two eggs are in the nest at 6:00. At 6:09.30 chatters and rough phrases come from Red-crown pair, and female flies down and settles on nest. Male stays nearby, singing faintly. She looks around occasionally, and finally champs bill a few times. 6:18.15 she rises somewhat, her abdominal feathers puffed out, and turns to face me. Her tail goes up about 20 degrees; then she rearranges her wings and subsides, the process taking about 20 seconds. She sits very high on the nest, blinking now and then as she looks around. She yawns and champs her bill once; then she champs again. Up, off, and down away north she flies silently at 6:30. Three eggs are in the nest."

Eggs of Red-throats were white. Six eggs averaged 25.7 by 17.6 mm.; the extremes were 26.3 by 18.1 and 24.6 by 17.1 mm. On the white background of eggs of Red-crowns were scattered speckles of pale cinnamon, averaging about a millimeter wide except where they coalesced, as they frequently did, in an irregular wreath about the large end; there were also a few superimposed spots of dusky brown of about the same average width, mostly in the wreath. In the one set measured, the first egg was 24.3 by 16.2 mm., the next 24.2 by 17.0 mm., and the third 24.3 by 17.4 mm.

INCUBATION

One female was twice seen to sit on incomplete sets, and once another female sat for 17 minutes during seven hours of observation, a few hours after she had laid the

second egg of a three-egg clutch. However, hatching times for young at a given nest were generally only a few hours apart, and on one occasion the last egg laid in a nest of Red-throats hatched earlier than the first two eggs.

The percentage of time females spent on the nest on Day 0 of incubation, the 24 hours after the last egg was laid, was 69.7 for Red-throats in 32.7 hours of observation and 61.4 for Red-crowns in 21.2 hours (all percentages are calculated by the method outlined by Skutch, 1954). The percentages for daylight incubation for the whole incubation period are 72.1 for Red-throats during 82.6 hours of observation and 68.5 for Red-crowns in 127.2 hours. Skutch (1954) found that many other tanagers incubated about 70 per cent of the hours of daylight.

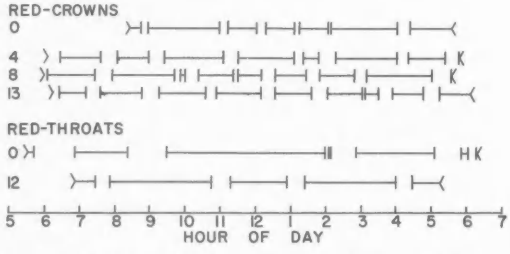

Fig. 3. Periods on and off the nest during incubation at four nests. The three records for the fourth, eighth, and thirteenth days of incubation are from one nest. Periods on the nest are shown by horizontal lines; periods off the nest are shown by blank spaces; > and < mark the beginning and end of a period of observation.

The average time Red-crowns spent on the nest per incubation period was 83.6 minutes for 59 periods; the average for 31 periods for Red-throats was 111.5 minutes. For Red-crowns, the high records were 204 and 188 minutes; for Red-throats, the longest periods were 315 minutes and more than 273 minutes. Skutch (1954) has noted only one longer period for a passerine; this was a record of 365 minutes for *Cyanocompsa cyanoides*, another bird subject to high rates of predation. The usual period for Central American tanagers is 20 to 30 minutes, although Skutch noted average periods of 76.3 minutes for *Eucometis penicillata* and 80 minutes for *Tangara gyrola*. The ant-tanagers spent long periods off their nests, an average of 43.2 minutes for 37 absences of Red-throats and an average of 38.5 minutes for 70 absences of Red-crowns. Consequently a female Red-throat would go to and from her nest only 12 times or so in a 13-hour day and a female Red-crown about 14 times. Infrequent visiting may reduce the possibility that a predator will detect the nest. The daily pattern of periods on and off the nest was variable, even at one nest (fig. 3).

When a shower swept across the forest, a female with eggs or young in the nest always returned to it by the time the first drops reached the undergrowth. She stayed low on her nest, gaping at times as if swallowing rain water, until the dripping slowed down a few minutes after the end of the shower.

A female returned to the nest either as her family foraged past it or after several nestward movements of up to a hundred meters at a time. At stops between such movements the family might forage for a minute or two, or strike out nestward after a brief look around. Near the nest the members of the family foraged in normal fashion. The female was often so inconspicuous that she slipped onto the nest without attracting my

attention. At times she hopped up the sapling and quietly dropped on the nest after a brief look at the eggs. On other occasions she flew directly to the edge of the nest from a few meters away, generally from below the nest. The others of the family foraged on as if the female had not dropped behind.

One female Red-throat called noisily before flying to the nest on several occasions; another called briefly once as she settled on the eggs. I never recorded any notes from female Red-crowns that were settling on the nest.

During incubation female ant-tanagers were quiet, and the slow movements of their heads were the only signs of life much of the time. Now and then a female gaped briefly, as if yawning. Rarely, when a ray of light chanced to illuminate her, I saw the slight quivering of tail and body due to breathing. At intervals her careful scrutiny of every passing bird or other movement was interrupted for a preening session. She half rose, leaving her brood patch open between her drooping ventrolateral feathers, and pecked vigorously at some part of her body as if after a parasite. After a few pokes, alternating with brief scrutinies of her surroundings, she either rocked down over the eggs or looked under her and poked at or between the eggs to turn them before settling. Often she worked her bill as she settled, perhaps removing debris from the edges of it. On the average, female Red-throats turned their eggs four times during each incubation period; the average of 216 intervals before, after, and between turnings was 22.0 minutes. Female Red-crowns turned their eggs twice, and the average of 156 intervals was 28.8 minutes. There was great variation, from turnings only a minutes apart to long incubation periods when the females did not turn their eggs at all. A female occasionally shifted her position on the nest. The tilt of her nest or branches near the nest edge might limit a female to one or two positions; otherwise she sat in several positions.

During the hot hours of midday a female often gaped for long intervals or stood over the eggs for several minutes at a time. Once I noted that the lower eyelid of a female Red-throat winked up over her eye for as much as a half minute. A female Red-crown that closed her eye in similar fashion kept her other eye open; she alternated, closing first one eye and then the other. Such eye-closing ceased abruptly when there was any nearby noise or movement. Mosquitoes occasionally annoyed the incubating birds, as sudden tosses of their heads demonstrated; a mosquito at times alighted on the forehead of an incubating bird and gorged itself.

Female Red-throats seemed more active than did female Red-crowns. The latter turned their heads slowly, a few degrees at a time, whereas female Red-throats more often turned their heads rapidly, through a large angle. Otherwise the two species behaved rather similarly and sat low in their nests with tails tilted slightly above the horizontal and heads held level. Female Red-crowns kept their crests folded to a narrow dark-bordered or dark line.

A family with an incubating female rarely led me anywhere near the nest, but on several occasions a family foraged past as I watched an incubating female from a blind. The male and immatures of a family showed no sign that they realized the female was nearby. On two occasions female Red-crowns darted off their nests past their mates on such visits, but on other visits females of both species stayed on the nest until long after their mates had departed. At times an incubating female rose and turned her eggs, or preened briefly, as her family passed. Rarely she gave a few faint notes, hard to distinguish from the louder calls of the foraging members of the family. Often a female moved her bill while her family passed.

Once an immature came up beside a female Red-throat; the two birds exchanged *wik* notes, the female gaped, and both female and immature left the nest. Once a male

Red-crown visited a female at the nest, spread his wings and tail in a variety of displays, held his bill open, and uttered faint notes. The female gaped and drew her head back but did not leave for another hour.

Each female looked around actively for one to several minutes before leaving the nest. After slipping off the nest the female generally flew below its level for the first few meters, but rose as she disappeared in the undergrowth. Twice I saw that she soon alighted and looked back toward the nest before stretching her wings and defecating. When I approached close to her nest, a female ant-tanager would flutter off through the forest and disappear. If I passed more than two or three meters away and made no moves toward the nest, she might crouch low and stay on the nest.

Female Red-throats when leaving their nests uttered faint *wik* notes as they passed my blinds but gave no louder calls. At some distance from the nests they broke into noisy chatters and rough scolds. On several occasions I was with the male and immatures of a family when such notes broke out some 100 meters distant. The birds immediately stopped foraging and flew higher in the undergrowth, uttering another burst of notes, and the whole group darted toward the commotion. Bursts of scolding, occasional day songs, and chattering drifted back to me. By the time I reached the source of the noise, the reunited family was foraging busily. If a family had been foraging at a swarm of army ants, all returned; for several minutes the tempo of *wik* notes and foraging activity was at a much higher level than before the female had arrived. If other members of a family had been close to the nest when the female left, rapid *waaj-tuk* notes and faint songs from the undergrowth near my blind made it apparent that the female and male joined quickly.

A female Red-crown was quiet in leaving her nest unless her mate were nearby. Then she flew under him with *chauf chauf* notes. Once a pair stayed and foraged near the nest, but more often the male chased the female off through the forest. Such a reunion was much more noisy and active if the female darted past the male at some distance from the nest. After the reunion the female foraged more busily than the male. She might give the *che-e-e* of the precopulatory ceremony now and then as she foraged, but usually she omitted wing fluttering and other actions of the complete ceremony. At times the male flew near his mate or chased her briefly, but I saw no attempt to copulate.

HATCHING OF YOUNG

Young had hatched in one nest of Red-crowns when I arrived at 7 a.m. on the thirteenth morning after the last egg was laid. At another nest of this species young did not hatch until the fourteenth night of incubation. The incubation period for one clutch of Red-throats was less than 12 days and 12 hours. Two young hatched in another nest during the fourteenth night of incubation; the last egg the female laid in this nest hatched after only 13 days and 7 hours. Table 3 lists the incubation periods of the two species.

Females were nearly always on their nests at the time eggs hatched. At three nests of Red-throats and at one nest of Red-crowns, females stayed on the nests for 210, 206, 159, and 222 minutes, respectively; but, at seven other hatchings of Red-crowns, females stayed on the nests for normal incubation periods and left between hatchings. A female might rise every few minutes to poke or peck at the eggs with great vigor, as did one female Red-crown, or be unusually quiet, as was a female Red-throat that made no noticeable move for an hour and a half.

After the young had hatched, the female pecked into the nest and swallowed small fragments of the shell. Occasionally she lifted her head and gulped down a large fragment after she had flattened it into a strip with her bill. Eating eggshells eliminates the necessity for special trips to carry them away, trips that might attract the attention of

TABLE 3

INCUBATION PERIODS FOR ANT-TANAGERS[1]

Species	First young	Second young	Third young
Red-crowned Ant-Tanager	13 days 7 hours	13 days 12 hours	Egg infertile
	?	13 7	?
	13 4	13 5	13 days 10 hours
	13 4	13 8	13 9
	?	?	13 12
Red-throated Ant-Tanager	12 5	12 6	Egg infertile
	13 7	13 8	13 10

[1] From hour of laying of third egg to hour of hatching of the young specified.

predators. Ordinarily the female remained on the nest for some time after eating the eggshells.

FEEDING THE NESTLINGS

One male Red-throat brought food twice to a nest while it was being built, but males were never seen to visit their nests while the young were hatching. Direct sight of the young was not necessary for one male Red-throat to start bringing food, for I recorded the following sequence some 15 minutes after the female first departed from the newly hatched young: "12:05 there is much noise moving up to 15 meters west of nest, with loud chatters and scolds. As female darts past me to the edge of the nest, the other three birds of the family perch around my blind and utter *wik* and *waij* frequently. The male sits with his body and tail feathers spread, food in his bill, on a stem in front of the blind; he looks around and toward female. She croons a soft warble, feeds young, spreads her abdominal feathers, and settles over the nestlings. But the male is insistent in his calling; she flies off at 12:05.55 and utters a few faint scolds as she passes her mate. He flies toward nest and . . . finally stretches down to young at 12:06.10."

Generally males were not so quick to feed their young as was this male. At one nest the male Red-crown was never seen to feed the young, although he visited them a few times and fed young in a later nest. Of 397 feedings of Red-throats, 131, or 33 per cent, were made by males; of 469 feedings by Red-crowns, 69, or 14.7 per cent, were made by males.

Eighteen successful feedings of young Red-throats, or 4.5 per cent, were made by immatures or by adult females other than the female parent; all records but one were at one nest. The immature at the latter nest fed the young at least as early as their fifth day in the nest and by their ninth day was feeding them at about the same rate as were the male and female.

The first meals for three young Red-throats in different nests came 40, 57, and 100 minutes after the females ate the eggshells; the first meals for three young Red-crowns came after 74, 130, and 170 minutes. On several occasions the tiny young was seen to gape when the female rose and poked downward into the nest a short time before leaving briefly to obtain food.

Very young nestlings were fed infrequently, but the rate of feeding increased as they grew older (fig. 4A). The average interval between feedings was 29.6 minutes for Red-crowns (417 intervals) and 21.2 minutes for Red-throats (366 intervals). The great activity of male Red-throats accounts for part of the difference between the two species.

When only one young was in a nest, the intervals between feedings were shorter than when two young were in a nest; when three young were present the intervals between

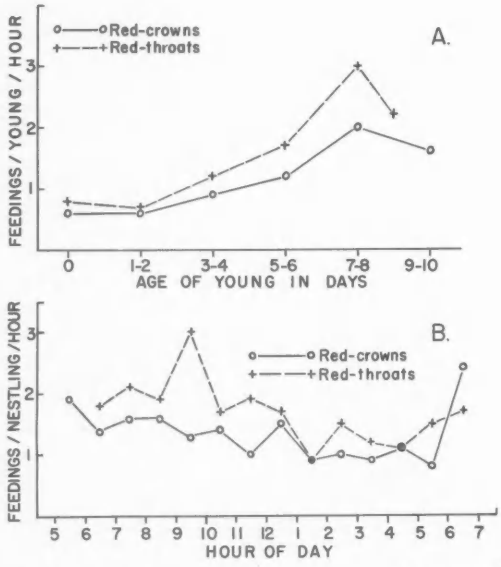

Fig. 4. A, changes in the rate of feeding as nestlings grew; B, rate of feeding young during the day.

feedings were the shortest. However, most of my records for only one young in a nest were in the late days of the nestling period, after the disappearance or departure of one or more nestlings, at a time when feedings were normally more rapid (fig. 4A). If the bias thus introduced is offset by recalculation (for example, from fig. 4A the feeding rate for Red-crowns on the eighth day is 3.2 times the rate on the first day; hence each interval for Red-crowns on the eighth day is multiplied by 3.2), the ratio between intervals for one, two, and three young becomes 2.4: 1.6: 1 for Red-crowns and 2.0: 1.6: 1 for Red-throats. These ratios are not the 3: 2: 1 ratio that might be expected, but are in agreement with the observations of Moreau (1947) that the rate of feeding is higher in larger broods but not in direct proportion to the number of young.

The rate of feeding was slightly less rapid in the afternoon than in the morning (fig. 4B), but the assertion of some authors that tropical birds stop feeding their young in midday because of the heat was not true for the ant-tanagers at Gallon Jug. The variability in feeding rates from hour to hour at six nests is indicated in table 4.

The female ant-tanager held food nearly hidden in her bill as she approached the nest. At each stop she looked around carefully. The brief passage of a breeze through the undergrowth, which rustled leaves and made other movement hard to detect, often coincided with the female's flight up into the nest sapling. If the nest were low, the female generally flew directly to its edge; but a few females, particularly those at two successful nests of Red-crowns, often halted for as much as half a minute in rigid poses on limbs below the nests. If the young had gaped when the female landed below the nest, they generally settled back and were quiet when the female finally ascended to the nest. But in the days just before departure of the young birds, particularly if two or three

TABLE 4

VISITS OF ANT-TANAGERS WHILE FEEDING YOUNG

Hour of day:	6	7	8	9	10	11	12	1	2	3	4	5	6
Red-crowns													
2 young, 0 days old													
(May 20, 2:53–6:18)									–	3	2	1	2
3 young, 5 days old													
(July 18, 11:55–6:30)						1	–	3	5	2	5	4	4
2 young, 9 days old													
(July 4, 6:08–6:25)	6	4	4	2	1	3	3	1	1	1	3	4	1
Red-throats													
2 young, 1 day old													
(June 15, 8:20–3:30)			–	4	–	1	3	–	2	–			
3 young, 5 days old													
(July 6, 9:19–6:11)				2	4	14	7	4	3	5	5	8	1
3 young, 9 days old													
(July 20, 6:03–4:25)	5	5	2	5	5	3	15	3	1	1	3		

were in the nest, their importunate gaping and squeaking left the female no choice but to break her stop off short.

As they approached their nests, female Red-crowns were ordinarily silent; but some female Red-throats gave every few seconds the faint calls normally used in foraging. If I was out of the blind when the female approached the nest, she called noisily, flew about, and turned back and forth on her perch. She did not drop or eat her food but refused to go to the nest while I was near it.

Male Red-crowns often warbled a liquid and irregular song and quivered their wings as they approached nests. Female Red-crowns accompanied by warbling males, or by day-singing and chattering males without food, often gave *chook* notes or faint chatters until they were only a few meters from their nests. As a female fed the young, the warbling of a male with food grew louder, more rapid, and more irregular; her movements became quicker, and finally she darted past the male with a faint *chauf chauf*, to forage and chatter nearby as the male, suddenly silent, darted to the nest. When a male arrived and found the female brooding, he warbled until she darted off past him after a few seconds of looking around and poking the young. Occasionally a male warbled near the nest for several minutes even when no female was present. Male Red-throats alternated low and deliberate day songs with faint *wik* notes until the females left the nests. However, females at times offset this comparative restraint by uttering a rapid stream of notes as they flew nestward ahead of their mates or as they flew past the males when leaving. Although males of both species often spread their body feathers and tail while singing, they compressed their feathers as soon as they flew to the nests. I never saw a male display his bright crest during a visit.

On the occasions when young were fed as a foraging family wandered past the nest, perhaps in company with the many other insectivores of a wandering forest flock, the usual calling and foraging activity was interrupted only by the ant-tanager that went to the nest.

Ordinarily the first downward poke with food, usually within a second after the adult reached the edge of the nest, resulted in the gulping movements of a young bird swallowing food. But when a parent Red-crown brought a large arthropod, the young generally had trouble eating it. Into one open gape after another the parent placed the food, crushed end foremost. Retrieving the arthropod quickly if it did not go down im-

TABLE 5

TIME REQUIRED TO FEED YOUNG

	Red-crowns	Red-throats
Feeding immediate	318 visits (68.5 per cent)	323 visits (82.2 per cent)
Feeding difficult (2+ seconds)	146 visits (31.5)	70 visits (17.8)
Average time to feed young	52 seconds	8 seconds

mediately, the parent crushed it still more by moving it back and forth in its bill. A low *chuk*, seemingly a soft version of the normal foraging call, usually stimulated one or more young to gape again. But after several attempted feedings the young became sluggish, and the *chuk* notes came louder and faster. A male might resume warbling and fluttering as he looked for open gapes; if he found none, he ate the food himself before departing. A female soon would settle over the young. At intervals she rose and crushed the food still more as she uttered the *chuk* note rapidly. One female finally fed a young bird an hour after she arrived. On a few occasions the female ate the food herself. Skutch (1954) found that Red-crowned Ant-Tanagers in Costa Rica had similar troubles feeding their young large arthropods.

Pairs of Red-throated Ant-Tanagers seldom (table 5) had as much difficulty feeding their young, perhaps because they generally brought smaller particles of food. The note corresponding to the *chuk* of Red-crowns was a faint *wik*, much like the ordinary call of Red-throats.

As soon as the young bird grasped the food, the adult ant-tanager champed its bill and looked around briefly. If the young began to swallow the food, the adult repeated champing as it looked at the young with one eye and then with the other. After 40.4 per cent of 463 feedings of Red-crowns and 38.8 per cent of 379 feedings of Red-throats, the young lifted its tail and emitted a fecal sac. The parent either ate the sac or flew off with it (fig. 5). Eating fecal sacs probably reduced the conspicuousness of the departure of the parent and, when the female stayed to brood, made it unnecessary for her to leave the nest.

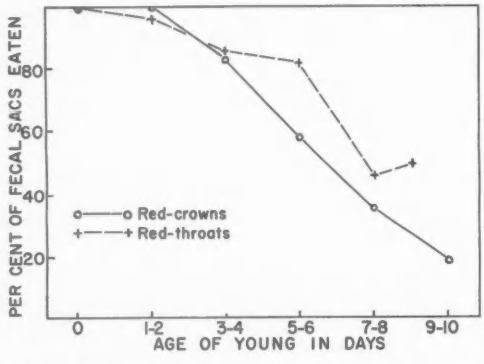

Fig. 5. Percentage of fecal sacs eaten by parent ant-tanagers.

A female often remained for some time after she fed the young. She looked at the young and the lining of the nest carefully between periods of scrutinizing the rest of her surroundings. Now and then she tapped lightly down into the nest, or pulled and pecked

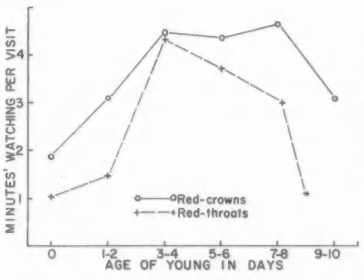

Fig. 6. Time spent by female ant-tanagers watching young after each feeding.

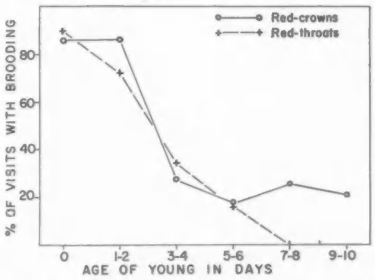

Fig. 7. Percentage of visits to nests by female ant-tanagers followed by brooding periods.

vigorously. Often she worked her bill after such sessions, which apparently were devoted to removing and eating tiny parasites, bits of food, fecal matter, debris, and fragments of the sheaths of feathers. One female Red-throat pecked at a dead young at intervals for several hours before she carried it away from the nest in her bill. Occasionally females of either species captured and ate one of the mosquitoes that hovered persistently around the young. When the young began to gape and call, the female left the nest.

The average time between feeding and departure from the nest or resumption of brooding was 3.6 minutes for female Red-crowns and 2.8 minutes for female Red-throats (fig. 6). The period of watching the young was often interrupted by the arrival of the male with food. Males seldom stayed and peered into the nest. Occasionally males of either species stayed as much as four minutes, but the average length of time the male remained at the nest was 40 seconds. Immature Red-throats usually waited only for fecal sacs: their average stay at the nest after feeding was 27 seconds.

After watching the young, a female of either species often lowered her abdominal feathers and hopped forward over the brood. A brooding female differed from an incubating female in her higher position, her more frequent shifting, and her behavior during her more frequent periods of standing. During such periods she often tapped at the

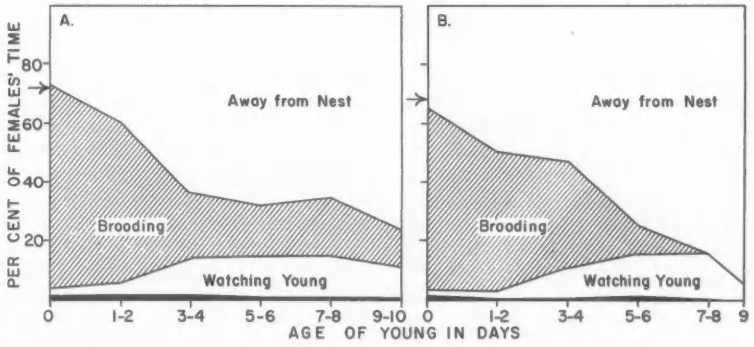

Fig. 8. Disposition of time by female Red-crowns (A) and Red-throats (B) during the hours of daylight. The arrows indicate the percentage of the daylight hours spent in incubating. The black areas indicate the time spent feeding young.

young or picked up bits of debris. If the young gaped before she settled, faint peeping notes continued under her. Large young thrust their heads through her feathers at such times and called and gaped whenever she moved. The increased activity of large young did not cause the average period of brooding to become shorter; instead, the per cent of visits that were followed by brooding periods became less (fig. 7) as the young grew older. Brooding periods were partly replaced by periods when a female watched young from the edge of the nest as they grew older (fig. 8).

The average brooding period for Red-throats was 34.8 minutes, and 59 records varied from 1.5 to 116.5 minutes; for Red-crowns, the average was 31.6 minutes, and 127 periods ranged from 15 seconds to 131.7 minutes. The average brooding period was much shorter than the average incubation period, even though brooding took nearly as much of the time of the females at first as had incubation (fig. 8). The average for 15 brooding periods of Red-throats on Day 0 (the period from hatching to the first dawn after hatching), was 23.9 minutes; for 50 periods for Red-crowns, the average was 34.4 minutes. The visits of males with food, and the gaping of young when females rose and pecked at them, interrupted periods of brooding. Occasionally females returned to nests and brooded without feeding young birds.

Before leaving the nest, an ant-tanager of either sex generally looked around carefully. Often the bird dropped in shrike fashion as it flew away. On a few occasions, I saw the adult stop ten to thirty meters away from the nest and look back toward it before flying on. Less often a parent hopped up or down in the nest sapling and paused for as much as several minutes before darting away.

GROWTH OF THE YOUNG

Young Red-crowns and Red-throats proved similar in their development. Because of extreme predation, few young could be examined, but the following notes should help future workers in determining the ages of nestling ant-tanagers to within two or three days.

In table 6 feather growth has been divided into five stages, which are represented by the letters D, W, P, B, and V: first, invaginations into the skin formed, but were noticeable only on a few tracts; dusky dots (D) soon formed at the bases of invaginations; the dots elongated into wedges (W) inside the feather follicles; pinfeathers (P) then projected as metallic-blue shafts; eventually the shaft tips acquired greenish pigment and split until they were like tiny camel's-hair brushes (B); soon the brushes expanded into vanes (V) as barbs separated from the central axes closer and closer to the bases of feathers. Lengths of feathers (in millimeters; or "short," "medium," or "long"—S, M, or L) and of the part of the length of each feather with open vanes (decimal preceding a "V") represent measurements from the points where feathers emerged from the follicles, not from points at the true bases of the feathers beneath the skin.

Newly hatched young had buffy brown down on several tracts: coronal, occipital, scapular, femoral, posterior dorsal, extreme posterior abdominal, greater secondary covert, and median secondary covert. The down was most conspicuous on the coronal lines, but it reached 9 mm. in length only on the dorsal tract. Slender filaments up to a millimeter in length became visible on the rectrices and on additional feathers of the abdominal tract as the down was pushed out on the tips of the pinfeathers. Although a few feathers of the wing of one well-fed young Red-throat were opening on Day 5, most feather debris was shed after Day 6. Since the debris remained in the lining of the nest, it was easy to tell from examination of an empty nest whether or not young had reached the age of seven days. The feathers opened serially from outermost to innermost in the secondaries, greater secondary coverts, and alulars; primaries opened in the reverse

direction, that is from 1 to 9. The greater primary coverts opened 5–4–3 and so on. The left and right wings of an individual often differed in the number of feathers open at any one time, although the order of opening of feathers was constant.

The gapes of young Red-crowns were red or orange, as is usual in the Thraupidae (Skutch, 1954); the gapes of young Red-throats were yellow at first but gradually became reddish. On Day 0 the bills of all nestlings were stubby and mottled pink. On Day 2 bills were becoming dusky; by Day 7 the mottling was nearly obscured by dusky pigment. The yellowish white angles of the gapes were retained, but the remainder of the bill became dark as it grew in size. The orange and fleshy feet anteriorly developed tarsal scutellation and a horn-pink color by Day 2. By Day 9 the legs were dusky in front, pink on the sides, and pale flesh-color behind; the claws were dark above but remained whitish below. Gradually the feet became as dusky as the feet of adults.

TABLE 6

FEATHER GROWTH IN YOUNG ANT-TANAGERS

	Age in days								
	2	3	4	5	6	7	8	9	10
WING FEATHERS									
Primary	LW	P	P	B	B	B	0.25 V	0.5 V	0.7 V
Longest (no. 4 or 5)		2–5	5–11	9–18	15–20	23–25	26–39	35–39	48
Secondary	LW	P	P	B	B	V	0.25 V	0.6 V	0.7 V
Longest (no. 1)				7–15	12–18	23–24	34–36	36–37	48
Greater covert	SW	P	P	B	B	V	0.25 V	0.6 V	0.7 V
Longest		2	4–6	7–11	8–15	17–18	19–25	18–25	20
Marginal	Few D	D	SW	W	P	SB	B-V	V	V
Alular	D-MW	P	P	P	SB	B-V	V	V	V
Longest		1.5–3	4–6	5–10	8–15	14–15	15–20	18–24	20
HEAD FEATHERS									
Frontal-coronal	D	D-SW	MW	LW	SP	MP	P	P	P-B
Occipital	D	D-SW	MW	LW	SP	MP	P	P-B	SV
Auricular	—	—	D	D	SW	P	P	P	P-B
Malar	—	—	D	D	SW	SP	SP	MP	P-B
Throat	—	—	—	—	D	D-W	D-P	D-P	D-B
BACK AND LEG FEATHERS									
Dorsal									
Cervical	D	SW	LW	SP	P	P	V	V	V
Mid-dorsal	D-W	MW	P	P (3)	P (5)	B	V	LV	LV
Pelvic	—	D	SW	LW	SP	P	SV	V	V
Scapular	D	D	D-SW	P (3)	P (5)	B	V	LV	LV
Femoral	D	D	MW	P (3)	P (4)	B	V	V	V
Crural	—	D	SW	MW	P (1)	B	V	V	V
Tail	—	—	—	D	MW	P (1)	P	P-B	SV
VENTRAL FEATHERS									
Breast	D	MW	LW-P	P	B (5)	V	LV	LV	LV
Abdominal	D	D	MW	P	P (3)	B	V	V	V
Anal circlet	—	—	—	D	W	P	SV	SV	SV
Undertail covert	—	—	D	D	W	B	SV	SV	SV
YOUNG EXAMINED IN DETAIL									
Red-crown	1	1	2	1	2	2	1	1	2
Red-throat	2	2	2	2	1	1	1	2	0

Nine young Red-throats from 5 nests and 6 young Red-crowns from 4 nests were examined. Young 0 days old showed no feathers; short wedges were on the primary, secondary, and covert tracts on Day 1. Lesser and median wing coverts were intermediate between marginals and greater coverts. For explanation of symbols see text, p. 494.

By Day 2 the formerly united eyelids were separated by slits up to a millimeter in length. On Day 4 the eye slits were nearly complete, and young opened their eyes at times. On Day 6, young kept their eyes open during their extended periods of preening and movement each time the female stayed after a feeding.

Newly hatched young were barely able to right themselves when inverted. On Day 2, young could right themselves readily, hold their wings and legs close to their bodies, and loosely grasp a stick or my finger. At this age young no longer gaped or peeped in the hand when I moved or blew upon them. On Day 3 and thereafter young commonly excreted when removed from the nest. On Day 4 and thereafter young clutched the nest when captured and huddled when in my hand; some yelled *weeah!* when taken from the nest. Young five days old or older gaped in my direction and cowered in the nest when I extended my hand toward them.

From a *peep* much like the call of many young birds, the notes of ant-tanagers became a brief *chee* or *chee-e-e-e* by the third day of life in the nest. Young squeaked variants of such notes rapidly during feedings. Loud *chut-chut-chip*! or "nest-leaving" calls were first uttered on the day before the first young bird left the nest and were given frequently when the parents were foraging nearby in the days that followed. Whenever the calls were uttered while the parents were out of sight, as on occasions when I held a fledgling inside my blind, both parents darted toward the calls at once. Possibly the calls may have served to keep the parents near the young during the critical period of departure from the nest. From Day 15 to Day 20 notes intermediate between the chatters of adults and the nest-leaving calls of young were heard from fledglings of both species. Young Red-throats gave calls intermediate between the *chee* and the scold of adults as early as Day 11; on Day 18 the scolds were still weak but like those of adults in other respects. From Day 18 to Day 36 a loud *chiat*!, intermediate in quality between the scold and the *chee* but more like the former in amplitude, was repeated rapidly by the juvenile as it followed its parent. Young Red-crowns, which usually sat hidden in leaves or vines three to ten meters above the ground waiting for parents to return, gave a faint *chie* as a location call from Day 10 to about Day 35. The *wik* of adult Red-throats was but a slight modification of the *chee* of the nestling, but the origin of the *chook* of adult Red-crowns is uncertain. The *chook* was first heard from a fledgling Red-crown on Day 27. Songs and calls of adult ant-tanagers are described in Willis, 1960*a*.

On Day 7, young Red-throats occasionally detected approaching parents by their *wik* calls and gaped while the parents were distant from the nest. At times a young bird uttered a nest-leaving call. The young preened actively, climbed over each other, and pecked or gaped at one another more and more frequently on days 8 and 9. Four young left two nests on Day 8. I caused the departure of two; the other two may have been ousted by a predator. Five young Red-throats left on Day 9. Young Red-crowns were similar to young Red-throats in feather development, but the former did not utter nest-leaving calls or start active movement in the nest until Day 9. They left the nest only on Day 10.

Young Red-throats and Red-crowns rarely fluttered their wings in the nest. Young which fell out of nests of Red-crowns on Day 7 refused to move when pushed. Young Red-throats eight or nine days old could barely hop and rested for long periods. On days 10 and 11 young of both species hopped and fluttered along the ground for longer periods and took shorter rests. On Day 13 a fledgling Red-crown fluttered as much as six meters after its parents, but it usually had to flap its wings and pull itself up to the top of a limb with its bill and neck when it alighted. On Day 18, fledgling Red-throats whirred directly and rapidly from limb to limb, and by days 20 to 25, young of both species flew fairly well.

During feedings, fledglings usually gaped and fluttered the tips of their wings but rarely squeaked. The competition among nestlings probably caused the vigorous squeaking in the nest after Day 3. Three nestlings in a nest were far more noisy when fed than were two nestlings, and a single nestling was quiet unless the parent hesitated before a feeding or had been gone a long time. Once, when a female tapped the gape of a 13-day-old Red-crown and pushed an insect down its throat with scarcely a break in her chattering at me, the young bird did not even move its wings.

A Red-throat about three weeks old visited a nest when the nestlings were in their fifth day and begged silently from the pair feeding them. This bird pointed its gape at the food, even when the morsel was in the beak of a nestling after the adult had departed. The female which accompanied this fledgling on following days may have been a second mate of the male at this nest.

The earliest that a young Red-crown was seen to dart after an insect was Day 27. On days 32 and 36 this bird was obtaining most of its own food, although it lacked the grace and agility of its parents. Immature Red-throats apparently became independent at approximately the same age. None was seen to be fed after Day 30, although one begged from a female on Day 39.

Bare shafts and gaps still showed in the wings of young ant-tanagers on days 10 and 11. At this age the dorsal and scapular feathers covered most of the back of the bird when it hunched in the normal sitting position. However, the head was bare except for a few areas of pinfeathers and small feathers, the midventral apterium was exposed from breast to anal circlet, and the flanks, the sides of the neck, and the thighs were bare. On Day 18 the faces of young birds still lacked covering. The heads of young Red-throats seemed shaggy and small until the postjuvenal molt, but young Red-crowns resembled the adult female in the feathering of the head long before the molt.

The length of the tail beyond the upper tail coverts was in the field the best indication of the age of a fledgling. The tail of each young first showed beyond the upper tail coverts about Day 13; on Day 22 the tail was about 30 per cent as long as the tail of a female parent; about Day 29, the tail was about 80 per cent as long as that of the adult bird, and on Day 36 it was as long as that of the adult bird, namely 50 mm.

The drab, brown plumage of one young Red-throat was unkempt on Day 52, as if it were molting. On Day 72, August 1, the throat of this bird was yellow, as is true of young in their first winter plumage. The brown color of the rest of the body had been partly replaced by the lighter shade of the first winter plumage. Fledgling Red-crowns had throats that were yellower than the throats of fledgling Red-throats or of female Red-crowns; but in several young Red-crowns, which were two months old in late July, I detected molt not by changes in the color of the plumage but by the ragged state of the plumage.

DEPARTURE FROM THE NEST

Young ant-tanagers are no better feathered when they leave the nest than are the nestlings of other tanagers several days before leaving. The early departure of young ant-tanagers may be a behavioral adaptation to predation. The noisy competition of the young for food as they grow older and the repeated visits of their parents to the same spot increase the chances that a predator will find the nest and capture the whole brood at once. But, as soon as young leave the nest, they can be secreted in separate spots and these hiding places changed at intervals. A hopping fledgling might be conspicuous during infrequent intervals of movement, but it is not much more conspicuous than several young preening actively in one nest. Covering the young during the relatively cool rains or nights in the tropics may be a problem with such early departure

from the nest, however. Two young Red-throats were secreted 20 meters apart after leaving one nest. But the sibling Red-crowns out of the nest were perched only a few meters apart on two occasions. Moreover, the tolerances of unfeathered fledglings to rain and chilling may be greater than one would suppose. It is not the danger of chilling but the inability of birds younger than eight days old to move about that probably sets the lower limit for the age of fledging.

When young left the nest, the female was always calling nearby. Otherwise the details of departure varied considerably. One female Red-throat found me examining a young bird. As soon as I had replaced the young bird and entered the blind she stopped her displays and darted to the edge of the nest; a few notes and a peck under the two huddling, silent nestlings stimulated them to give a few nest-leaving calls and hop over the edge of the nest. A female Red-crown watched her actively preening young for three minutes after a seven-minute brooding period; then she hopped off into the nearby limbs and started calling *chuk*, the usual feeding call, as she looked at the nestlings. Soon one fledgling hopped out. After it was led away the female and male returned, and I recorded: "Female calls frequently from bush about 3 meters SE of nest. Young calls *chee* and *chip*. Finally young stops preening and turns toward female, answering each *chuk* with faint *chee* notes as it looks back and forth for way up onto nest edge. Once young tries ascent; flutters as falls back into nest. Young looks again, finally hops on edge at 9:37. Female turns her tail toward it, calls *chuk* less often. Young looks for place to land. 9:38.45 it jumps and flutters down, clinging for a moment to the tip of a palm leaf before it drops to the ground, 3 meters below the nest. Parents lead young bird away, as before."

At two other nests of one pair of Red-crowns, the young birds fell out of the nest when seven days old. One nest was knocked down by a heavy rain. The rim of the second nest was so low on one side that the young bird may have fallen out when it backed up to the edge of the nest to emit a fecal sac. Both young birds were fed on the ground. When they were replaced, the female fed them in the nests after looking for them on the ground. At one nest of Red-throats one young bird and at another nest three young in succession left by jumping out of the nest as soon as the females flew to nearby trees after feedings.

After young ant-tanagers left the nest they were led away by their parents. The female fluttered back and forth from twig to twig just ahead of a fledgling, fluttering from one side of it to the other in a kind of "shielding flight" (Skutch, 1955) every time it moved. Female Red-crowns kept up a stream of faint feeding calls and other notes; female Red-throats gave *wik* calls, faint scolds, and other sounds. The male usually flew from branch to branch ahead of and above the female and called occasionally as he looked around. Once an immature Red-throat joined such a caravan and flew back and forth ahead of the male. At another nest of Red-throats a second female left her well-grown immature and led off one of the young while the parents were leading the other two away. Young of either species, if over eight days old and able to climb, were enticed up on twigs or vines arising at an angle from the ground.

If I came near one of these young and then retired to a distance, it was soon led off to another perch. When I emerged from a blind and captured a fledgling, I encountered the first distraction displays recorded for any members of the tanager family (Skutch, *in litt.*). At the first squawk of the young bird the female uttered a loud chatter as she darted past my hand. Then she hopped rapidly over the ground and low twigs nearby, her wings held up or down or one up and one down. Her tail was spread fully and dragged the ground or was held high. Red-throats gave prolonged scolds, while Red-crowns typi-

cally uttered falsetto chatters. If the male were present, he displayed as vigorously as the female. Once an immature Red-throat joined a pair, and three birds displayed around me. Each call from the young bird inspired a fresh display, but eventually the parents stopped and watched me from nearby limbs, where they turned rapidly from side to side and called noisily.

Some parents hardly displayed at all. Others added variations to the displays just mentioned. Two different male Red-throats were seen to fall to the ground from about two meters up, give a loud call as they hit, and hop away from me while performing the usual display. Once a female Red-throat drooped her body and tail feathers, quivered her lowered wings, and turned her head listlessly as she looked toward her toes. Such displays made the parent seem crippled or sick.

The use of these displays only at a time when the fledglings were near or on the ground, which few other young tanagers ever reach, fits in well with the observation of other authors that most such displays are performed by ground-nesting birds. Later, when the young were higher in the undergrowth, I did not note distraction displays.

Young Red-throats over 18 days old were led through the forest in a characteristic fashion by their parents. As the male scolded, the female uttered a series of rapid *week* notes and low scolds until the less wary young bird followed. As soon as it took wing, one or both parents crisscrossed its path in a shielding flight so effective that I rarely saw the young alight even on a few occasions when it alighted in plain sight. My eye was attracted by one parent or the other, which alighted in full view before the young alighted at all. Once the young bird started moving, it and the rest of the family moved so rapidly that I detected the birds for minutes at a time only by a stream of faint notes from the distant undergrowth. Young Red-crowns of about this age sat quietly and were led away only after I retired to some distance. They were ordinarily secreted farther above the ground when I found them than were young Red-throats, in keeping with the generally higher foraging range of Red-crowns (Willis, 1960*b*).

The male Red-throat from a territory near one nest repeatedly brought food to two fledglings, although it was persistently driven away by the male parent.

PREDATION, RENESTING, AND CLUTCH SIZE

Destruction of the eggs and young of ant-tanagers was as great as has been reported by several authors (see Moreau, 1940; Skutch, 1945) for other birds of the tropical forests. Of 53 nests of ant-tanagers, only 8 or 15.1 per cent produced one or more fledglings. Only 16 young were fledged from at least 147 eggs laid, for 10.9 per cent success. One nest was knocked down by a heavy rain, one by a falling limb; the other unsuccessful nests were robbed by predators. The disappearance of eggs and young from nests of other species on the study area was similarly frequent. Since on an adjacent area that I rarely visited, three out of three nests of ant-tanagers were successful, it may be that my intensive observations of nests on the study area attracted the attention of predators.

In over 530 hours of watching nests of ant-tanagers from blinds, I never saw a predator take the eggs or young. Possibly much of the predation came at night, but perhaps predators were inhibited from going to a nest by my presence.

Skutch (1945) thinks snakes are the major predators. Once a pair of Red-crowns chattered long and violently at a snake (*Oxybelis*), and the female left her nest to join in the chatter. Whenever ant-tanagers and the small birds of a wandering flock encountered such snakes, they scolded for minutes at a time. Undoubtedly various mammals and birds rob nests at times. Motmots (*Momotus momota*) approaching close to nests aroused ant-tanagers to more violent reactions than did any other species except such

a hawk as *Micrastur ruficollis*. Reactions of one pair of Red-crowns and of one family of Red-throats to motmots were as follows:

"*June 3*—[3 eggs in nest of Red-crowns]—One motmot flies down to a perch about one meter on the other side of the nest from me. Female ant-tanager hops off eggs and flutters along nest limb with wings down and tail spread. Male flies up; both yell, and finally attack and drive motmot off.

"*June 23*—[2 small young in nest of Red-throats]—3:51 two motmots fly up near nest, and female ant-tanager flattens out and becomes motionless . . . she presses wings flat on rim of nest and lowers her head and body as much as possible . . . At 4:40 scolds and faint day songs approach from northwest. The male and one immature ant-tanager fly up above my blind, scolding noisily, at 4:47. Female has not moved noticeably since 3:51. At 4:52 male and immature flutter around one motmot and drive it off southeast. Then two come back and scold near other motmot. At 4:54 they drive it off southeast. Male and immature fly back and give *wik* calls near the nest as the female rises and looks down at the young for the first time in over an hour." [The young were gone the next day.]

Whatever the sources of destruction of nests may be, it is probable that the nesting activities of ant-tanagers are adjusted to them. The great caution ant-tanagers ordinarily displayed in approaching and leaving their nests has been noted in discussions of incubation and the feeding of young. The wide spacing of feedings, and the unusually long periods on and off the nest during incubation, may have resulted from the danger to the young or eggs posed by frequent visits, as Skutch (1949) suggests. He has noted that many other tropical birds visit their young infrequently and bring large food items on such visits. However, factors other than predation may have caused this slow feeding rate. Ant-tanagers probably spent much time traveling to and from their nests over their large territories except when the young were ready to leave and food was obtained near the nests. It may be that tropical birds have a more difficult time finding food than non-tropical birds. Even though northern birds go to the tropics when northern woods do not provide enough food, the great number of species in such a forest as that at Gallon Jug may mean that the available supply of food for each species is reduced.

The rapidity of the renesting of ant-tanagers may be a response to predation. Averages of less than a week for nest construction, of 15 or 16 days for egg laying and incubation, and of 9 to 10 days for feeding nestlings add up to an extremely brief period of nesting. Young of other species of tanagers use their nests at least two days longer (Skutch, 1954). A complete nesting of Red-throats required only a month. Red-throats ordinarily started building a new nest only one or two days after the destruction of the contents of an old one, although most Red-crowns and some Red-throats delayed up to a week or two between nestings. One female Red-throat attempted five nestings between April 25 and June 17; I inferred at least two more from her behavior before I left on August 2. Other females were less prolific because some of their nests lasted more than a few days. Several females evidently attempted at least five nestings.

Despite constant renesting from April to August, only two out of the ten pairs of Red-crowns in the central part of my study area had a surviving fledgling when I left. Only two out of eleven families of Red-throats had young out of the nest after three months of nesting. One of the latter families produced two broods; two young from one nesting were about 60 days old on July 31, and one from a later nesting was about 38 days old. The two broods were probably the offspring of two females. A similar case of two broods from a family outside my study area has been noted in the discussion of the care and feeding of young. The 32-day old young bird of the second pair of Red-throats on my study area followed the male on July 27 while the female incubated two eggs of the next brood. No Red-crowns on the study area reared two broods; but a pair on an adjacent area had a juvenile about 40 days old with them on August 1, the day when two young left the nest. High rates of predation, and the low clutch sizes of tropical

species, probably account for the finding of Davis (1946), corroborated by my observations at Gallon Jug, that "the number of young birds in the tropics does not at any time reach the high levels of the temperate regions." The predation-induced slow recruitment of young birds may insure that the food supply in summer is not over utilized by a large crop of young in a restricted period.

Although it may be theoretically advantageous for young ant-tanagers to leave the nest at an early age for reasons already noted, mortality of young out of the nest was rather high. When I left, only four out of seven young Red-crowns to leave the nest on my study area and elsewhere were still alive (average age of survivors, 19 days); only two out of nine young Red-throats were still alive, at ages of 19 and 73 days. Most of the young that disappeared did so within a few days after leaving the nest.

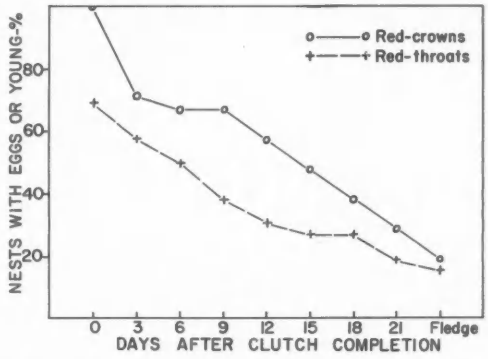

Fig. 9. Percentage of nests of ant-tanagers still containing eggs or young at various times after completion of clutches; figures are based on 21 nests of Red-crowns and 26 nests of Red-throats. Young hatched 12 to 14 days after completion of clutches and left the nest 21 to 24 days after completion of clutches.

Eggs of Red-crowns were lightly speckled, and eggs of Red-throats were white. Ever since it was first observed that most birds that nest where their eggs are hidden lay eggs lacking pigment while most birds that nest where eggs are uncovered on leaving the nest lay colored eggs, it has been repeated that pigments make eggs less conspicuous. Why should ant-tanagers lay "conspicuous" eggs? It may be that, if a nest is situated on a predator "route," it is an advantage to an ant-tanager to have the set of eggs destroyed early, thus giving more time for a renesting that may be off the predator routes, rather than after several weeks of effort have been expended raising doomed young. Figure 9 gives some support for this hypothesis, since the main destruction of the eggs of ant-tanagers may be seen to fall within the period of egg laying and the three days thereafter. It is to the advantage of a repeatedly nesting species to show a low curve on such a graph, granted that the end point is as high as possible.

The eggs disappeared from eight nests of Red-throats. At some nests eggs were destroyed on the day of laying. A female Red-throat never incubated the remaining eggs of a clutch in which even one egg had been destroyed; she laid the other eggs of the clutch and then deserted the set, which at times remained in the nest several days before a predator took it.

SUMMARY

At Gallon Jug, British Honduras, each pair of Red-crowned Ant-Tanagers (*Habia rubica*) under observation nested from late March to August or later in 1957; Red-throated Ant-Tanagers (*Habia gutturalis*) began nesting in late April.

Nests of Red-throats were loose and leafy structures which needed support underneath. The thin but compact nests of Red-crowns, woven of epiphyte rootlets, rhizomorphs, and similar materials, were sometimes pensile.

Females of the two species differed less in their methods of hunting for material and of working on nests than in their choices of materials. Once a nonbreeding bird of a family of Red-throats helped the female build a nest. Nests were nearly complete after three mornings of work. The interval between the start of building and the laying of the first egg averaged seven days for Red-crowns and six days for Red-throats.

Three eggs, laid on successive mornings, formed the usual clutch. Females incubated about 70 per cent of the hours of daylight during incubation periods of 12 to 14 days. Thereafter the time spent brooding decreased rapidly from the level of 70 per cent.

Of the feedings of Red-throats, 33 per cent were made by males; but only 14. 7 per cent of the feedings of Red-crowns were made by males. Nonbreeding birds in two families of Red-throats helped feed young. The rate of feeding increased as young grew older. The rate was faster in larger broods, but not in direct proportion to the number of young. Feeding was only slightly less frequent during the afternoon hours than in the morning.

Young of Red-crowns and Red-throats were quite similar in growth of feathers, even though Red-crowns left the nest when ten days old and Red-throats left when eight or nine days old. Young of both species were small and poorly feathered after leaving the nest and could barely fly for two or three days thereafter. Adults gave distraction displays when fledglings were approached. Juveniles attained full tail length about four weeks after leaving the nest.

One pair of Red-crowns apparently raised two broods, and one pair of Red-throats had eggs in one nest while the male fed a young bird out of the nest. Two families of Red-throats raised two broods each, but in these cases each male was probably bigamous. One male Red-crown had two mates and two nests at the same time. However, most pairs did not raise even one brood, even though several pairs probably nested more than five times during the three or four months in which I observed breeding. Unknown predators robbed 43 of 53 nests of ant-tanagers.

Probably many aspects of the nesting of ant-tanagers are influenced by the high danger of predation in tropical forests. Very long attentive periods alternated with long breaks and thus reduced the number of arrivals and departures per day. Females and their mates tended to approach nests very carefully. Eggshells and fecal sacs were eaten, at least when young were small. Such behavior eliminated the necessity of carrying away conspicuous objects or of making special trips to do so. Young Red-crowns were fed large arthropods, which the younger nestlings had trouble swallowing; but the large size of food particles may have made frequent feeding unnecessary. Perhaps the premature departure of nestlings reduces their vulnerability to predators, but there was rather high mortality of young out of the nest in this study. It seems likely that the short length of each nesting cycle makes it possible for ant-tanagers to produce young birds despite frequent destruction of nests.

Some aspects of the nesting of ant-tanagers seem inadaptive. Ant-tanagers used cup-shaped nests, not covered nests; the latter would perhaps take much time to build, thereby decreasing the number of nestings possible in a season. Ant-tanagers placed nests in

open sites, not in dense growth; but open sites far outnumber dense tangles in the high forest favored by ant-tanagers over dense second growth. Moreover, while foraging as well as while nesting, ant-tanagers kept out of dense tangles, perhaps because dense growth restricted their movements and made them more vulnerable to predators.

Possibly predation and low clutch sizes account for the slow recruitment of young into tropical populations.

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FROM FIELD AND STUDY

Supplemental Data on the Sex Ratio in Nestling Boat-tailed Grackles.—In a recent paper (Condor, 62, 1960:34–44), I have shown that the nestling sex ratio in the Great-tailed Grackle (*Cassidix mexicanus prosopidicola*) in Texas does not exhibit significant deviation from a normal Mendelian ratio of 50:50 (table 1). This finding raised a serious doubt concerning the validity of an earlier report by McIlhenny (Auk, 54, 1937:274–295, and Auk, 57, 1940:85–93) of a nestling sex ratio strongly unbalanced in favor of females (2.51 females to 1 male) in the Boat-tailed Grackle (*Cassidix major major*) in Louisiana. But, since it was recently discovered that the two grackles are separate genetic systems, being full species rather than merely races as previously supposed (Selander and Giller, Condor, 63, 1961:29–86), it seemed desirable to examine the nestling sex ratio in *C. major*.

TABLE 1

SEX RATIO IN NESTLING GRACKLES

Form and locality	Number of nests	Number of nestlings	Males	Females
Cassidix mexicanus prosopidicola				
Central and SE Texas	65	136	72	64
Cassidix major major				
Sabine Refuge, Louisiana	28	76	38	38
Mixed sample[1]				
Near Vinton, Louisiana	14	32	14	18
Totals	107	244	124	120

[1] Nestling not identified to species; probably includes equal numbers of both species.

Between June 2 and 10, 1959, 21 nestlings of *C. major major* were collected at the Sabine National Wildlife Refuge, Cameron Parish, Louisiana. An additional sample of 55 nestlings was obtained in the same area on June 1 and 2, 1961. Dissection of these 76 nestlings showed a precisely equal sex ratio (table 1), thereby confirming my previous supposition that McIlhenny's figures were based on a faulty method of sex determination in which sex was judged by relative body size rather than by examination of gonads.

In both species of *Cassidix* it is now apparent that the existing imbalance in the tertiary (adult) sex ratio, in which females outnumber males, results not from a corresponding imbalance in the primary or secondary sex ratios but from differential mortality in the sexes beyond the nestling stage of development. The significance of this fact in relation to sexual dimorphism and the promiscuous, colonial breeding system of these grackles will be discussed in a forthcoming report on the biology of *Cassidix*.

I wish to thank Mr. Kent E. Myers, Director of the Sabine National Wildlife Refuge, for assistance in obtaining nestling grackles. This study was supported by the National Science Foundation (G–15882).—ROBERT K. SELANDER, *Department of Zoology, The University of Texas, Austin, Texas, June 5, 1961.*

Golden-winged Warbler in Southern California.—On October 23, 1960, a small warbler, conspicuous by a yellow patch on each wing and by its habit of hanging head downward in chickadee fashion from the branches, was sighted in the top of a sycamore tree in Montecito, Santa Barbara County, California. The next morning (October 24) the same or a similar bird was collected within two hundred feet of the place where it had been seen the previous day. Mr. Egmont Rett, Curator of Birds and Mammals at the Santa Barbara Museum of Natural History, who prepared the specimen, pronounced it a first-year male Golden-winged Warbler (*Vermivora chrysoptera*), very fat and in good plumage. The skin is deposited in the Santa Barbara Museum collection (no. 4326). A search of the literature at hand failed to reveal a reference to this warbler from California. Dr. Alden H. Miller has informed the writers (correspondence, January 3, 1961) that he does not know of a prior record of occurrence of the Golden-winged Warbler in California or in any other Pacific coast state. —CHARLES H. RICHARDSON and ALICE I. RICHARDSON, *Santa Barbara, California, February 16, 1961.*

An Early Reference to Torpidity in a Tropical Swift.—Torpidity in birds has been of great interest for centuries, but authentic accounts of this phenomenon are rare and are confined to only a few species. McAtee (Amer. Midl. Nat., 38, 1947:191–206) gave a virtually complete list of references on avian torpidity up to that date, and Bartholomew, Howell, and Cade (Condor, 59, 1957:145–155) and Howell and Bartholomew (Condor, 61, 1959:180–185) cited publications on this subject appearing since McAtee's compilation. A previously overlooked account of torpidity in a bird seems worthy of mention for the sake of completeness.

Almost one hundred years ago, Osbert Salvin described the Greater Swallow-tailed Swift (*Panyptila sancti-hieronymi*) as a new species (Proc. Zool. Soc. London, 1863:190–192). His specimens were obtained from the highlands of Guatemala. In his account of the new form, Salvin wrote that "In July of last year (1862) I had the satisfaction of having brought to me alive, by Mr. Carter of San Gerónimo [Vera Paz, Guatemala], two birds . . . . They had been caught by an Indian under a rock near the village of Matanzas, in the mountains. The birds, though apparently uninjured, were quite sleepy, not attempting to fly; the only energy they exhibited was by making their powerful claws meet in my fingers when I endeavoured to secure them."

There can be little doubt that Salvin had obtained two swifts in a torpid condition. His comment that "the only energy . . . exhibited" was the strong grip of the feet corresponds well with our own observations on torpid White-throated Swifts (*Aëronautes saxatalis*). As Salvin's birds were evidently captured in a roosting place at a high elevation, it is likely that they had been exposed to air temperatures as low as those at which torpidity has been noted in other swifts. However, it would be worth while for biologists to look for evidence of torpidity in tropical swifts of lowland as well as highland distribution. Large species in particular must have to expend considerable energy to remain airborne continuously for many hours, and heavy rains of long duration such as often occur in the tropics could make food gathering difficult or impossible for extended periods of time. A reduction of energy expenditure by hypothermia during roosting would therefore be advantageous in warm lowland areas as well as in the cool highlands.—THOMAS R. HOWELL, *Department of Zoology, University of California, Los Angeles, California, June 2, 1961.*

Accipiter pectoralis, a Synonym of Accipiter poliogaster.—In all recent works on the genus *Accipiter* in South America two widespread but rare forms of the South American lowland forest are listed as species, namely *Accipiter pectoralis* (Bonaparte, 1850) and *Accipiter poliogaster* (Temminck, 1824). The latter is a plainly colored form, leaden black above, darker on tail and crown, with obscurely barred tail; below it is uniformly grayish white, becoming white on the throat. *Accipiter pectoralis* is entirely different in color, with a pronounced pattern, which, it has often been remarked, is surprisingly similar to that of the adult of the Ornate Hawk-Eagle, *Spizaëtus ornatus*. It is blackish above, the feathers narrowly bordered with white, becoming brownish on the wings, and with the tail barred with black and gray. The sides of the head and neck and a collar on the hind neck and interruptedly across the breast are rich chestnut. The remainder of the underparts are white, conspicuously marked with scattered black bars.

The entirely different coloration of these two birds is presumably responsible for the fact that in such standard works as Peters' Check-list and Hellmayr and Conover's Catalogue other species are placed between them. Nevertheless, careful comparison of *pectoralis* and *poliogaster* will show that they are identical in every respect of size and external anatomy. Furthermore, the differences in their distribution as indicated in various check-lists might easily be, and in fact is, the result of their rarity. So far as I know Bertoni was the only author to indicate a close relationship between these two accipiters; in fact he thought that *pectoralis* was the female of *poliogaster*. It was later shown that this was not the case and thereafter almost everyone regarded the two as perfectly distinct and not necessarily very closely related.

In 1951 (Hornero, 9:258–262) my colleague, A. G. Giai, reported *Accipiter poliogaster* from Argentina for the first time. He also described in detail a specimen taken on January 18, 1950, in the course of our joint explorations of Misiones Province, which he considered to be the hitherto unknown immature of *poliogaster*. He found its plumage pattern to be somewhat like that of *pectoralis* and concluded that these two species were related and that in the field it would be impossible to tell the male of *pectoralis* from what he considered to be the young of *poliogaster*. After careful renewed

study of this intermediate specimen as well as other material of both supposed forms, totaling eleven in all, I have concluded that Giai did not go quite far enough and that "*pectoralis*" is in fact only the immature plumage of *poliogaster* and that the name *pectoralis* is a synonym. The chief reason why this has not been appreciated earlier, aside from the previous lack of specimens molting from the one into the other, is the fact that this immature plumage is so distinct and unusual that it is difficult to believe that it can be the forerunner of the plainly colored adult of *poliogaster*. Although there seems to be no other *Accipiter* with quite such a striking contrast between adult and immature, it should be pointed out that in most species of the genus in which the adult is without spots or barring the immature is so marked. *Accipiter b. bicolor* is a good example in the New World and there are others among the numerous species of *Accipiter* in the East Indies and New Guinea.

The species *poliogaster* is a rather unusual *Accipiter*, not only as regards its immature plumage, but also in its relatively short tail and stocky proportions. Some might prefer to give it a genus of its own, as was done long ago by Cabanis who applied the name *Dinospizias* to *pectoralis*. The difficulties of subdividing the genus *Accipiter* are well known and I certainly recommend leaving *poliogaster* in it.

I am indebted to D. Amadon who compared my material with that in the American Museum of Natural History and agreed in the conclusion stated above. Further details and photographs will be included in my forthcoming treatise on the avifauna of Misiones.—WILLIAM H. PARTRIDGE, *Buenos Aires, Argentina, June 19, 1961.*

An Occurrence of the Laysan Albatross on the Northwestern Coast of Oregon.—On July 13, 1960, a Laysan Albatross (*Diomedea immutabilis*) was found washed ashore on the beach between Gearhart and Peter Ihrdale State Park, Clatsop County, Oregon, by William M. Wallace. Due to the state of deterioration it was prepared as a skeleton and no determination of sex was possible. I find no previous mention of this species occurring on the Oregon coast in the literature. The specimen is now in the United States National Museum (no. 431309). I would like to thank Herbert G. Deignan of the National Museum for confirming the identity of the specimen.—LEON A. FREDRICH, *Portland, Oregon, May 14, 1961.*

Flight Speeds of Some Small Birds.—Numerous observers have reported speeds of flying birds, but the measurements have usually been made under conditions in which it was impossible to measure the speed and direction of the wind. The importance of correcting for air movement is shown by the fact that in the speed range of most small birds, failure to make appropriate correction for a wind described by meteorologists as merely a "gentle breeze" may cause calculation of the air speed of the bird to be in error by as much as 50 per cent. The following measurements were made under conditions of known wind speed.

Birds were trapped at Orinda, California, between February 4 and April 5, 1961, and were taken within two hours to a large, corrugated iron, highway drainage pipe 56 inches in diameter. The birds were released singly about 30 feet back in the dark culvert and were photographed with a motion picture camera as they emerged from the pipe. The camera ran at a speed of 68 exposures per second, determined by photographing a long, swinging pendulum of known frequency. As each bird emerged from the culvert, it flew across a 3-foot-wide piece of cardboard ruled with lines one inch apart, thereby making it possible to measure the bird's progression in successive exposures. A large mirror adjusted to the appropriate angle to reflect a second 1-inch grid perpendicular to the first appeared at the edge of each photograph. The position of the bird's image in this mirror enabled one to calculate the bird-to-background distance, and from this to correct for the fact that the bird was closer to the camera than was the background grid. The culvert opened into a sheltered ravine into which wind seldom penetrated. Nevertheless a sensitive wind indicator was placed so as to appear in each photograph. Only on one morning was there a detectable breeze, which was a cool draft emerging from the pipe at 2 miles per hour. Correction has been made for this in the measurements given in table 1.

On one morning the light was so weak that the image reflected in the mirror could not be seen in the photographs, and consequently the background-to-bird distance could not be calculated. In these examples I have assumed that the bird was in the middle of the possible range of distances. This assumption introduces the possibility of an error as great as 10 per cent, so I have placed these values in parentheses. The other measurements are probably accurate to within a few per cent.

When the birds were released in the culvert, some obviously were confused and flew almost at stalling speed toward the exit. Others flew immediately at what appeared to be full speed out of the exit. No claim can be made that these are actually top speeds for the species, but the faster speeds listed are undoubtedly close to those of alarmed birds under their natural conditions and may actually be maximum speeds of the individuals tested. For the passerine species, the faster speeds obtained by this photographic method do not differ greatly from some of the published estimates made by other methods. A speed of 23.8 miles per hour, however, for the Allen Hummingbird (*Selasphorus sasin*) is only half of the 45 miles per hour reported by Hayes for an automobile-paced Ruby-throated

TABLE 1

SPEEDS IN MILES PER HOUR

(Each figure represents a different bird)

White-crowned Sparrow (*Zonotrichia leucophrys*)—19.1, 13.3, (23, 21, 19, 16, 14).
Golden-crowned Sparrow (*Zonotrichia atricapilla*)—20.9, 19.0, 17.2, 15.6, 15.4, 13.5, 13.4, 13.0, 11.5, 10.8 (26, 24, 19, 18, 18, 16, 11).
Song Sparrow (*Melospiza melodia*)—15.9 (21).
Fox Sparrow (*Passerella iliaca*)—9.8.
Brown Towhee (*Pipilo fuscus*)—22.0 (14).
Allen Hummingbird (*Selasphorus sasin*), males—23.8, 18.2, less than 34.9.[1]

[1] Inertia is so great in the camera mechanism that full film speed is not attained until about the tenth exposure of each series. This bird first appeared in the fifth exposure, and so his recorded speed is too high by an unknown amount.

Hummingbird, *Archilochus colubris* (Auk, 46, 1929:116) and much less than half of the 55–60 miles per hour reported by Allard for another automobile-paced Ruby-throated Hummingbird (Auk, 51, 1934:84). These earlier estimates seem to be much too high, however, in view of Greenewalt's recent discovery that Ruby-throated Hummingbirds cannot progress against a 30 mile per hour wind (National Geographic, 118, 1960:673), and in view of Van Riper's photographically-obtained estimates of 18 to 29 miles per hour for Broad-tailed Hummingbirds, *Selasphorus platycercus* (in C. L. Stong, 1960, The Amateur Scientist, Simon and Schuster, p. 178). It seems likely that the cruising speed, and perhaps top speed, of hummingbirds is nearer to 25 miles per hour than to the 50 assumed in my earlier estimate of the maximum flight range of Ruby-throated Hummingbirds (Condor, 52, 1950:145). A second refinement of the assumptions used for that estimate is also possible. On the basis of the data existing at that time I assumed that the migrating bird carried one gram of fat available as fuel. Odum and Connell (Science, 123, 1956:892) have found that Ruby-throated Hummingbirds just before migration contain 2.1 grams of fat. By assuming that 2 grams of this are utilized during a non-stop flight (instead of 1 gram), and that the cruising speed is 25 miles per hour (instead of 50), the earlier estimate of flight range in still air remains unchanged at 385 miles. Probably the weakest of the remaining assumptions used in obtaining this estimate is that the metabolic cost of linear flight is the same as for hovering. It is also possible that dehydration rather than fat consumption limits the length of the flight.—OLIVER P. PEARSON, *Museum of Vertebrate Zoology, University of California, Berkeley, June 15, 1961.*

Tricolored Blackbirds Nesting in Jackson County, Oregon.—Gabrielson and Jewett in collecting material for their book on the birds of Oregon found many old records of Tricolored Blackbirds (*Agelaius tricolor*) in Oregon. These records were all unsupported by specimens. Both authors spent some time in Jackson County, Oregon, but failed to find the species. Johnson Neff and I saw a few at different times in Klamath County and found a nesting colony on the Copco Ranch near Agency Lake in 1933. We collected nine males (Condor, 35, 1933:234–235). At that time these were the only specimens for Oregon.

Sometime in the summer of 1956 I saw 15 or 20 Tricolored Blackbirds on a lawn near the Cottage Street bridge in Medford, Jackson County, Oregon. In May of 1957 several hundred of these black-

birds were feeding in a field of vetch about 3 miles east of Medford. On June 2, 1958, Thomas McCamant discovered a nesting colony of Tricolored Blackbirds numbering about 1500 on Bear Creek, just east of Central Point in Jackson County (Audubon Field Notes, 12, 1958:379). These nests were in blackberry vines. I visited this colony on June 21 and found all nests with young birds. In 1959 we were unable to find the nesting colony.

On May 30, 1960, while making a bird count with a group of Medford bird watchers I found a large colony of Tricolored Blackbirds nesting in the cattails in a pond near the Rogue River in the Camp White area. We estimated there were at least 1800 birds present. I returned on June 2 and collected three males and three females, and also three nests with three eggs each. The specimens are now in the Carl Richardson collection of Southern Oregon College and the Alex Walker collection at Tillamook, Oregon.—CARL RICHARDSON, *Trail, Oregon, May 25, 1961.*

Association of Trogons and Monkeys on Barro Colorado.—Chapin (Birds of the Belgian Congo, Part II, Bull. Amer. Mus. Nat. Hist., 1939:352) has referred to African hornbills and Asiatic drongos that feed on insects driven from vegetation by bands of foraging monkeys. Stott (Auk, 64, 1947:130) has reported a similar association between Fairy Bluebirds and long-tailed macaques on Mindanao in the Philippine Islands.

On February 10, 1961, the authors recorded a further example of this method of insect procurement by birds, on this occasion by trogons, in the Canal Zone Biological Area, Barro Colorado Island. At approximately 2 p.m. on a hot, sunny, and still afternoon, four Slaty-tailed Trogons (*Trogon massena*) were encountered as they moved through the forest in the wake of a troop of five white-throated capuchins (*Cebus capucinus*) near Fuertes House. We watched both trogons and monkeys through binoculars and saw the birds repeatedly sally out to hawk insects that had been disturbed by the feeding monkeys. As the capuchins progressed through the forest, the trogons individually exchanged one perch for another near the area presently occupied by the monkeys. The fact that four trogons, two males in adult plumage and two females, of the same species at times occupied perches in a single tree seemed remarkable. In observing 12 species of American and Asiatic trogons at large, we have not seen more than two adult trogons of the same species jointly pursuing the same activity. On this occasion, the unusual presence of four birds in the same area did not seem to indicate flocking or any noteworthy degree of compatibility but rather a coincidental interest in a common food source. In one instance, one of the male trogons dove down and drove the other from a perch that appeared more advantageously situated from the standpoint of simian activity and the resulting disturbance to insect life.—KEN STOTT, JR., and C. JACKSON SELSOR, *Natural History Museum, San Diego, California, March 17, 1961.*

Bird Records from San Luis Obispo County, California.—The following records of birds in San Luis Obispo County in central California are unusual or new with respect to place or season. On October 1, 1955, a Parasitic Jaeger (*Stercorarius parasiticus*) was observed over the tidal flats of Morro Bay for several minutes. Identification of the bird, in the dark phase, was confirmed by Mr. Eben McMillan. The only previous record for this area seems to be that of Grinnell and Hunt (Condor, 31, 1929:63).

On July 22, 1956, a male Common Goldeneye (*Bucephala clangula*) was observed for nearly half an hour by Richard Pimentel and myself at Cambria; it was in a small slough at the mouth of Santa Rosa Creek.

Starlings (*Sturnus vulgaris*) were first noted in San Luis Obispo County in 1958 by McMillan (Condor, 61, 1959:157). Since then a breeding colony was discovered by Bill Wallace at a point about two miles northeast of Santa Maria. A visit to this locality on May 27, 1960, revealed three nests, in holes in dead sycamore tree limbs. Five adults were observed at one time, and young could be heard squealing from one hole. On June 27, 1960, Mr. Wallace brought in an adult female, with partly enlarged ovary, which was prepared as a study skin.

A second specimen was taken on February 9, 1961, at the same locality. It was a male, one of two birds seen, and it had slightly enlarged testes. Both specimens are now in the California State Polytechnic College collection.

Mr. Wallace told me, when he brought in the second specimen, that there were also Starlings in the Cuyama Valley, and a flock of about 50 had been seen near San Simeon.—ARYAN I. ROEST, *Biological Sciences Department, California State Polytechnic College, San Luis Obispo, California, March 25, 1961.*

Winter Record of a Tree Sparrow in Central Alaska.—A Tree Sparrow (*Spizella arborea*) visited our feeding station near College, Alaska, many times between January 21 and April 20, 1961. It was seen first during unusually mild weather when record-breaking maxima of 34, 45, 47, and 33°F. were reported in Fairbanks for the period from January 19 to 22. Until the first of April the sparrow fed in the company of a Slate-colored Junco (*Junco hyemalis*) on weed seeds, food scraps, oats, and other items in snow-free areas directly under spruce trees in mixed aspen-spruce forest. Unofficial minimum temperatures of about —20°F. were noted at the feeding station early in February and in mid-March. Between March 4 and March 20 the ground was covered with fresh snow so that the feeding areas used by the Tree Sparrow were hidden. The bird was not seen during this period.

On April 1 Tree Sparrow songs were heard near the feeding station but not again until April 16 and 17, when two individuals were heard. The first migrant Tree Sparrows were seen in the Fairbanks area on May 6, 1961.

No previous records of Tree Sparrows are known to us for central Alaska between November 1 and March 30. Gabrielson and Lincoln (Birds of Alaska, 1959:785–788) list only one record for the entire state for the period from December to March; a specimen was taken at Wrangell, southeastern Alaska, on January 16, 1919. The bird we saw could have been in the Fairbanks area all winter, or it might have miscalculated spring and flown north from a wintering area at lower latitudes. The nearest regular wintering area is southern British Columbia (Munroe and Cowan, A Review of the Bird Fauna of British Columbia, 1947:224). Even there they are uncommon. Central Alaska certainly seems to offer little chance for the survival of Tree Sparrows through the winter, as snow usually covers essentially all of the ground from October until April.—JUDITH S. WEEDEN, *Department of Biological Sciences, University of Alaska,* and ROBERT B. WEEDEN, *Alaska Department of Fish and Game, Box 425, College, Alaska, May 10, 1961.*

NOTES AND NEWS

The University of California and the Museum of Vertebrate Zoology will serve as hosts for the annual meeting of the Cooper Ornithological Society in April of 1962. Local members of the Society are making arrangements for sessions on April 20 and 21 with a field trip on Sunday, April 22.

In 1963 the annual meeting of the Society will be at the University of Texas at the invitation of the University of Texas, the Texas Ornithological Society, The Travis Audubon Society, and the Wilder Wildlife Foundation. Dates will be announced later.

The Division of Biological and Medical Sciences of the National Science Foundation announces that the next closing date for receipt of basic research proposals in the life sciences is January 15, 1962. Proposals received prior to that date will be reviewed at the spring meeting of the Foundation's advisory panels and disposition will be made approximately four months following the closing date. Proposals received after the January 15, 1962, deadline will be reviewed following the summer closing date of May 15, 1962.

The Museum of Comparative Zoology has just reprinted Volume III of the late J. L. Peters' "Check-list of Birds of the World." This volume, long out of print, lists the Columbidae and Psittacidae, and related families. The only other volumes available are V, VII, and IX, but if sufficient interest is indicated we hope to reprint additional volumes.

With the cooperation of specialists throughout the world, work is progressing rapidly toward completing the unpublished volumes. Volume XV, containing the Ploceidae, Sturnidae, Oriolidae, Dicruridae, Paradisaeidae, Corvidae, and others, is in press and should be ready early in 1962. The proposed sequence for the remaining volumes is: X, XII, XIV, XIII, XI, VIII.—Raymond A. Paynter, Jr.

Members are requested to forward unusual or "out of range" records of the Clark Nutcracker for the fall and winter of 1961–1962 to John Davis, Hastings Reservation, Carmel Valley, California.

Several thousand eggs collected over a period of about forty years by the late Frank M. Phelps of Elyria, Ohio, have been presented to the University of Massachusetts by Mrs. Phelps. The collection, to be known as the Frank M. Phelps Memorial Egg Collection, will be catalogued in the Zoology Museum and will be available for study at the University. Western areas represented in the collection are Alberta and the Chisos Mountains in western Texas. It is anticipated that this will form the nucleus of a growing collection.—L. M. Bartlett.

The Cooper Ornithological Society's A. Brazier Howell Award of $150 is given each year for the best paper presented at its annual meeting by a member who does not possess the Ph.D. degree in biological sciences. The Society's Harry R. Painton Award of $500 is presented every other year at the Annual Meeting for the best paper appearing in The Condor during the preceding four years. This latter award will next be made in 1963.

Louis Agassiz Fuertes Research Grants, established in 1947, are devoted to the encouragement and stimulation of young ornithologists. One particular desire is the development of research interests among amateur ornithologists. Any kind of ornithological research may be aided. Recipients of grants need not be associated with academic organizations. Each proposal is considered primarily on the basis of possible contributions to ornithological knowledge.

An anonymous donor gave $500 to found the fund; later donors have provided some $600. The Council of the Wilson Ornithological Society has added funds as necessary to provide at least one $100 grant annually.

Application forms may be obtained from Harvey I. Fisher, Southern Illinois University, Carbondale, Illinois. Completed applications must be received by March 1, 1962.

The new edition of the International Code of Zoological Nomenclature is due for publication in November, 1961. The Code, in its new form, consists of a volume of about 200 pages and has English and French parallel texts on facing pages, English and French glossaries, Index, Introduction by Dr. Norman Stoll and a Preface by Professor J. Chester Bradley. The price is one pound sterling, post free. Orders should be addressed to the Publication Office, The International Trust

for Zoological Nomenclature, 19 Belgrave Square, London, S.W. 1.

Recent major works published include the following: Bannerman and Lodge's volume X of the Birds of the British Isles (Oliver and Boyd Ltd.) dealing with the second part of the Shorebirds; David W. Johnston's Biosystematics of American Crows (University of Washington Press); Bellrose, Scott, Hawkins, and Low's Sex Ratios and Age Ratios in North American Ducks (Illinois Natural History Survey); and Yamashina's Birds in Japan, a Field Guide (Tokyo News Service Ltd.).

At the meeting of the American Ornithologists' Union in Washington, D.C. in October of 1961, the Brewster Award was made to Harold Mayfield for his book on the Kirtland Warbler. The officers elected for 1962 are: President, George H. Lowery, Jr.; First Vice-President, John T. Emlen, Jr.; Second Vice-President, Roger Tory Peterson; Editor, Donald S. Farner; Secretary, Lawrence H. Walkinshaw; Treasurer, Charles G. Sibley. Newly elected council members are Eugene Eisenmann, W. Earl Godfrey, Olin Sewall Pettingill, Jr., and S. Dillon Ripley. Fellows elected were M. A. Carriker, Jr., E. Thomas Gilliard, Kenneth C. Parkes, and Allan R. Phillips. Persons designated elective members were Donald J. Borrer, Paul A. Johnsgard, Karl W. Kenyon, Peter Marler, Andrew J. Meyerriecks, Walter P. Nickell, Frank Richardson, J. Dan Webster, and Glen E. Woolfenden.

Programs of divisional meetings of the Cooper Ornithological Society in recent months included the following: "Birds and Animals of Australia," by William H. Moore, in Los Angeles on May 31; "Aspects of the Biology of the Orange-fronted Parakeet," by John William Hardy, in Los Angeles on September 27; "The Classification of Birds as Indicated by Protein Structure," by Charles G. Sibley, in Berkeley on May 4; "Geographic Variation in the White-crowned Sparrow," by Richard C. Banks, in Berkeley on October 5.

James P. Chapin delivered the Lida Scott Brown lecture in ornithology at the University of California at Los Angeles on June 5, 1961, speaking on "Bird Study in Central Africa."

INDEX TO VOLUME 63

By Jane R. Durham

A

Accipiter, 178–179, 505–506
  bicolor bicolor, 506
  bicolor pileatus, 179
  cooperii, 178
  pectoralis, 505– 506
  pileatus, 179
  poliogaster, 505–506
Acrocephalus arundinaceus, 282
Aechmophorus occidentalis, 227, 264
Aegithalos caudatus, 213
Aëronautes saxatalis, 505
Agelaius, 59, 68
  phoeniceus, 58, 183, 218, 282, 330, 340, 356
  tricolor, 330, 507
Aix sponsa, 209
Akepa, 179
Akialoa, Kauai, 180
Alauda, 418
  arvensis, 418
Albatross, Black-browed, 257, 260
  Black-footed, 185–197, 257–258, 260, 262–263, 304–311
  Laysan, 185–197, 260, 263, 304–311, 506
  Light-mantled Sooty, 257, 260–261
  Shy, 261
  Wandering, 257, 260–261
Alderson, George, inland occurrences of the red phalarope in Oregon, 97
Alderton, Cora C., the breeding cycle of the yellow-bellied seedeater in Panama, 390
Alectoris, 123
  graeca, 111–127
  rufa, 111
Amadon, Dean, relationships of the falconiform genus Harpagus, 178
Amakihi, 180
Amazilia tzacatl, 396, 405
Amazona autumnalis, 404
Amphispiza bilineata, 266
Anabacerthia striaticollis, 405
Anas, 366, 368, 383
  acuta, 361
  discors, 404
  platyrhynchos, 351–364, 365–385
Anderson, Anders H., and Anderson, Anne, life history of the cactus wren. Part IV: development of nestlings, 87
Anhinga, 404
  anhinga, 404
Ani, Greater, 210
  Groove-billed, 210
  Smooth-billed, 202, 210, 405
Anianiau, 180
Anser, 401
Antbird, Dusky, 406
Anthus pratensis, 324
  trivialis, 217
Antshrike, Barred, 406
  Fasciated, 406
Ant-Tanager, Red-crowned, 479–503
  Red-throated, 201, 219, 479–503
Antvireo, Plain, 406
Antwren, White-flanked, 207
Apapane, 180
Aphelocoma, 234–245
  coerulescens, 148, 213, 234–236, 239, 331
  coerulescens cactophila, 239, 240, 244
  coerulescens californica, 234–235, 238–239, 242
  coerulescens cana, 239
  coerulescens caurina, 234–235, 237–239
  coerulescens hypoleuca, 239–240
  coerulescens immanus, 234, 237–239
  coerulescens insularis, 240
  coerulescens obscura, 234, 238–239
  coerulescens oocleptica, 234–235, 237–239, 244
  coerulescens superciliosa, 234–235, 238–239, 244
  gracilis, 242, 243
  ultramarina, 213, 234, 243
  ultramarina arizonae, 243
  ultramarina colimae, 242–243
  ultramarina couchii, 243
  ultramarina gracilis, 242–243
  ultramarina potosina, 240–243
  ultramarina sordida, 204–241
  ultramarina ultramarina, 240–241, 243
  ultramarina wollweberi, 241–243
  unicolor, 243
  unicolor unicolor, 242
  wollweberi, 241, 243
Aptenodytes fosteri, 200
Aquila chrysaëtos, 114
Araçari, Collared, 203, 211, 405
  Fiery-billed, 207, 405
Aramides cajanea, 404
Archilochus, 3–4, 10–11, 22, 26
  alexandri, 3–13, 21–26
  colubris, 4, 10, 323, 507
  violajugulum, 10
Ardea herodias, 98
  herodias herodias, 98
Argya malcolmi, 214
Arremonops conirostris, 406
Artamus maximus, 217
Atthis calliope, 17
Auklet, Cassin, 415, 456
  Rhinoceros, 456–473
Aviceda, 178
Avocet, 203, 402

Avocet, European, 209
Aythya affinis, 209, 404
valisineria, 265

B

Babbler, Jungle, 214
Large Gray, 214
Balanosphyra formicivora, 211
Banks, Richard C., and Johnson, Ned K., a review of North American hybrid hummingbirds, 3
Barbet, Pied, 211
Prong-billed, 405, 407
Red-headed, 405
White-eared, 211
Bartholomew, George A., and Howell, Thomas R., temperature regulation in Laysan and black-footed albatrosses, 185
Baza, 178
Bittern, Least, 404
Blackbird, Brewer, 58, 101, 162–177, 182–183
European, 203, 205, 215–216, 270, 272, 282–283, 288, 290
Redwinged, 58, 183, 202, 218, 220, 281–282, 284, 330–331, 335–336, 340, 356–357
Rusty, 165
Tricolored, 330–334, 336–337, 507–508
Bluebird, Eastern, 200–202, 204–206, 215, 281
Fairy, 508
Mountain, 215
Western, 215
Bobolink, 215
Bobwhite, 97, 272, 294, 299, 324
Bonasa umbellus, 97
Booby, Blue-faced, 261
Brown, 207, 209, 261
Bower Bird, Satin, 324
Bowles, John, and Richardson, Frank, records of the rarer native forest birds of Kauai, Hawaii, 179
Bowman, Robert I., late spring observations on birds of South Farallon Island, California, 410
Brachyramphus marmoratum, 456
Brant, Black, 418
Branta, 401–402
bernicula, 418
canadensis, 209
nigricans, 418
Brotogeris jugularis, 404
Brownell, Katharine A., and Hartman, Frank A., lipids in the locomotor muscles of birds, 403
Bruce, James A., pomarine jaeger in Mount Rainier National Park, 342; first record of European skylark on San Juan Island, Washington, 418
Bubo virginianus, 469
Bubulcus ibis, 404
Buccanodon leucotis, 211
Bucephala clangula, 508
Bunting, Indigo, 220, 281, 284, 341–342, 403, 406
Lazuli, 341–342
Reed, 282
Snow, 147
Bushtit, Black-eared, 202–203, 213
Common, 214
Buss, Irven O., correction, 183
Butcherbird, Pied, 217
Buteo harlani, 98
jamaicensis, 98
platypterus, 404
solitarius, 342
swainsoni, 266
Butorides virescens, 208
Bycanistes subcylindricus, 211

C

Cacique, Yellow-billed, 407
Calcarius lapponicus, 147
Calidris canutus, 180
Callipepla squamata, 294, 340
Calocitta formosa, 213
Calothorax lucifer, 10
Calypte, 3, 10, 13, 15, 22, 26
anna, 5, 7–13, 15–26
costae, 3–5, 7–10, 12–17, 22–25
Camptorhynchus labradorius, 380, 384
Campylopterus hemileucurus, 405, 407
Campylorhynchus brunneicapillus, 87–94
zonatus, 214
Canvasback, 265
Capella megala, 417
Caprimulgus europaeus, 210, 278
vociferus, 289
Cardiff, Eugene A., savannah sparrow breeding at Big Bear Lake in the San Bernardino Mountains of California, 97; two new records of birds for California and notes on species of the Imperial Valley and Salton Sea area of California, 183
Cardinal, 200–202, 204–208, 215, 219–220, 246–256, 270–272, 274–277, 281–282, 284–285, 290–291
Carduelis cannabina, 220
Carpodacus cassini, 418
mexicanus, 147, 220, 266, 323, 387, 410
purpureus, 418
Casmerodius albus, 404
Cassidix, 29–30, 33, 37, 45, 47, 51–52, 55, 57–63, 66, 68–70, 73–74, 76–77, 79–80, 504
major, 29–32, 34–35, 37–41, 44–51, 53–62, 64–81, 504
major major, 31, 33–34, 37–38, 40–44, 46, 50, 52–53, 54, 56, 81, 504
major torreyi, 31, 33, 37, 44, 50–54
major westoni, 31, 33
mexicanus, 29–35, 37–51, 53–64, 66–81
mexicanus graysoni, 41–42, 52–53, 80–81
mexicanus major, 29
mexicanus mexicanus, 29–31, 41–45, 52, 54, 62, 81

mexicanus monsoni, 31, 62, 81
mexicanus nelsoni, 41–43, 52–54, 80–81
mexicanus obscurus, 31, 40, 42, 52, 54, 62, 81
mexicanus peruvianus, 81
mexicanus prosopidicola, 29–31, 38–39, 41–47, 52–56, 62, 69, 80, 81, 504
nicaraguensis, 30, 50, 80
palustris, 30, 31, 50, 79–80
Catbird, 215, 271–274, 276–277, 281–282, 284–285, 290–291
Cathartes aura, 419
Centurus, 211
pucherani, 405
rubricapillus, 405
Cephus columba, 415, 457
Cercomacra tyrannina, 406
Cerorhinca monocerata, 456–473
Certhia brachydactila, 214
Ceryle torquata, 405
Chachalaca, Chestnut-winged, 403–404
Chaetura, 338
pelagica, 210, 338
Chaffinch, 137, 220, 270, 288
Charadrius alexandrinus, 209
semipalmatus, 181
Chasiempis sandwichensis sclateri, 180
Chen, 401
Chickadee, Mountain, 205, 213
Chiromachaeris coronata, 345, 348, 350
Chlidonias niger, 341
Chloroceryle amazona, 405
americana, 405
Chlorospingus ophthalmicus, 406
Chondrohierax uncinatus, 404
Chordeiles acutipennis, 405
minor, 278
Chough, White-winged, 213
Christman, Gene M., painting of hybrid hummingbirds, opp. 3
Ciccaba nigrolineata, 405
Circus cyaneus, 116
Cistothorus platensis, 172
Clangula hyemalis, 418
Claravis pretiosa, 404
Clark, George A., Jr., and Humphrey, Philip S., pterylosis of the mallard duck, 365
Coccothraustes coccothraustes, 220
Coccyzus americanus, 210
erythropthalmus, 210
Cochlearius cochlearius, 404
Colaptes, 215
cafer, 340
Colibri thalassinus, 323
Colinus virginianus, 97, 113, 272, 294, 324
Collocalia, 338
Columba, 452
albalinea, 404
livia, 210, 452
speciosa, 404
subvinacea, 404
Columbigallina talpacoti, 404, 454
Contopus virens, 273
Coot, European, 209
Coragyps atratus, 200, 212
Corapipo leucorrhoa, 406
Corcorax melanorhamphus, 213
Cormorant, Brandt, 411–412, 414
Double-crested, 412, 414
European, 200, 202, 209
Great, 209
Olivaceous, 403–404, 407
Pelagic, 414
Corvus, 212
brachyrhynchos, 112, 212
corax, 212, 474
frugilegus, 279
monedula, 212
palliatus, 242–243
ultramarinus, 237, 240, 243
Coturnix coturnix, 404, 451
Cowan, I. McT., and Cowan, Garry McT., the Amur barn swallow off British Columbia, 419
Cowbird, Bronzed, 183
Brown-headed, 58, 183, 220, 410
Cracticus nigrogularis, 217
Crake, White-throated, 404
Creeper, 179
Garden Tree, 214
Crocethia alba, 181
Crotophaga, 204
ani, 210, 405
major, 210
sulcirostris, 210
Crow, 112
American, 212
Crypturellus soui, 404
Cuckoo, Black-billed, 210
European, 214
Guira, 210
Yellow-billed, 206, 210
Cuculus canorus, 214
Cyanerpes cyaneus, 217, 406
lucidus, 406
Cyanocitta cristata, 213
stelleri, 143
superciliosa, 234, 236–238, 243
ultramarinus, 240, 243
Cyanocompsa cyanoides, 486
Cyanocorax dickeyi, 213
unicolor, 242–243
Cyanolesbia, 178
Cymbilaimus lineatus, 406
Cypseloides niger, 338

D

Dacnis cayana, 217
Dacnis, Blue, 203, 217
Turquoise, 217
Damophila julie, 405
Davis, Donald G., western grebe colonies in northern Colorado, 264; notes on a colony

of Forster terns at Timnath Reservoir, Colorado, 341
Davis, John, some seasonal changes in morphology of the rufous-sided towhee, 313
Delichon urbica, 212
Dendrocygna, 370
Dendroica, 349
auduboni, 349
castanea, 349
coronata, 349
discolor, 419
occidentalis, 349
pensylvanica, 410
petechia, 206, 220
striata, 349
townsendi, 349
Dinospizias pectoralis, 506
Diomedea cauta, 261
exulans, 257
immutabilis, 185–197, 260, 263, 304, 311, 506
melanophris, 260
nigripes, 185–197, 257–258, 263, 304, 311
Dolichonyx oryzivorus, 215
Dove, Barbary, 455
Blue Ground, 404
Diamond, 452–453
Gray-chested, 404, 407
Inca, 450–455
Mourning, 205–206, 210, 215, 271–272, 276–277, 281–282, 284–285, 324
Oriental Collared, 455
Ring, 417
Rock, 200–201, 210
Ruddy Ground, 404
Rufous-breasted Quail, 404
Rufous-naped, 404, 407
Scaly, 450–455
Talpacoti, 454
White-tipped, 404
White-winged, 205, 210
Dovekie, 338
Dryocopus lineatus, 405
Duck, Labrador, 380
Mallard, 351–364, 365–385
Wood, 204, 209
Duff, C. V., Malaspina's early California ornithological report, 340
Dulus dominicus, 217
Dumetella carolinensis, 215, 271, 274
Dunlin, 180
Dysithamnus mentalis, 406

E

Eagle, Bald, 267
Golden, 114
Eckelberry, Don R., painting of Brazilian manakins, opp. 345
Egret, Cattle, 403–404, 406–408
Common, 404, 407
Snowy, 404, 407
Elaenia frantzii, 406
Elaenia, Greenish, 406
Mountain, 406
Elanus, 178
caeruleus, 209
Elepaio, 180
Ely, Charles A., Cassin finch and pine grosbeak in west-central Kansas, 418
Emberiza schoeniclus, 282
Empidonax difficilis, 410
minimus, 181
traillii, 91, 181, 283
Eremophila alpestris, 266, 284, 415
Ereunetes, 181
mauri, 181, 183
pusillus, 181, 183
Erithacus rubecula, 137, 216, 270
Erolia alpina, 180
bairdii, 181
ferruginea, 182
minutilla, 181, 183
ruficollis, 182
temminckii, 182
Escalante, Rodolfo, occurrence of the Cassin race of the peregrine falcon in Uruguay, 180
Estrilda, 452
Eubucco bourcierii, 405
Eucometis penicillata, 486
Euphagus, 58–61, 68
cyanocephalus, 58, 69, 78, 101, 162–177, 182–183
Euphonia, Tawny-bellied, 207
Eurocephalus rüppellii, 217
Eynon, Alfred E., and Leopold, Aldo, avian daybreak and evening song in relation to time and light intensity, 269

F

Falco columbarius, 178
peregrinus, 98, 180
peregrinus anatum, 180
peregrinus cassini, 180
sparverius, 112, 342
Falcon, Barred Forest, 403–404
Peregrine, 98, 180
Fennell, Chester M., occurrence of the oystercatcher and Curlew sandpiper in Korea, 182; recent records of birds in Korea, 417
Finch, African Weaver, 101
Cassin, 418
House, 147–148, 206–207, 215, 220, 266, 323, 387, 410–411
Purple, 418
Fisher, Harvey I., the hatching muscle in North American grebes, 227
Flamingo, American, 202, 209
Greater, 200
Flatbill, Eye-ringed, 406
Flicker, Red-shafted, 340
Flycatcher, Ash-throated, 421–449
Boat-billed, 406–407
Great Crested, 214, 281, 284

Least, 181–182
Nutting, 421–449
Olive-sided, 410
Pied, 216
Spotted, 214
Streaked, 178, 406–407
Western, 410, 411
Traill, 91, 181, 283, 289
Foliage-gleaner, Scaly-throated, 405
Fowl, Scrub, 209
Fredrich, Leon A., an occurrence of the Laysan albatross on the northwestern coast of Oregon, 506
Fregata magnificens, 209
minor, 262
Frigate Bird, Great, 262
Magnificent, 207, 209
Fringilla coelebs, 137–138, 220, 270
Frings, Carl, egg sizes of Laysan and black-footed albatrosses, 263
Frings, Hubert, and Frings, Mable, some biometric studies on the albatrosses of Midway Atoll, 304
Fruitcrow, Purple-throated, 406
Fulica atra, 209
Fulmar, 339
Fulmarus glacialis, 339

G

Gallinula chloropus, 209
Gallinule, Common, 201–202, 209
Florida, 201, 209
Gallus domesticus, 101
gallus, 101
Garrulus californicus, 237
sordidus, 234, 240, 243
Genelly, Richard E., and Morejohn, G. Victor, plumage differentiation of normal and sex-anomalous ring-necked pheasants in response to synthetic hormone implants, 101
Geopelia cuneata, 452, 453
Geothlypis trichas, 282, 410
Geotrygon chiriquensis, 404
Giller, Donald R., and Selander, Robert K., analysis of sympatry of great-tailed and boat-tailed grackles, 29
Glaucidium brasilianum, 483
Gnatcatcher, Tropical, 201, 205, 216
Goldeneye, Common, 508
Goldfinch, Lesser, 410
Goose, Canada, 204, 209, 401
Gould, Patrick, J., territorial relationships between cardinals and pyrrhuloxias, 246
Grackle, Boat-tailed, 30, 81, 504
Bronzed, 207
Common, 52, 79, 207, 218
Great-tailed, 30, 81, 504
Nicaraguan, 30
Slender-billed, 30
Grassquit, Blue-black, 391
Grebe, Eared, 227–233
Horned, 227, 229–231, 233
Least, 403–404
Pied-billed, 227–233, 264
Red-necked, 227–231, 233
Western, 227–233, 264
Grefe, Robert E., and Wolf, Larry L., Brewer blackbird nesting in eastern Michigan, 182
Grosbeak, Black-headed, 206–207, 215, 220
Pine, 418–419
Rose-breasted, 203, 220, 406
Grouse, Red, 282
Ruffed, 97
Sharp-tailed, 171
Guillemot, 209
Pigeon, 415, 457
Guira guira, 210
Gull, Black-headed, 101
California, 339, 356, 476
Glaucous, 414, 474–478
Glaucous-winged, 457, 462, 477
Herring, 324
Silver, 262
Western, 411–412, 414–415
Gullion, Gordon W., and Gullion, Ardelle M., weight variations of captive Gambel quail in the breeding season, 95
Gygis alba, 466

H

Habia gutturalis, 219, 479–503
rubica, 479–503
Haematopus bachmani, 414
ostralegus osculans, 182
Hand, Ralph L., and Hoffmann, Robert S., recent shorebird records for Montana, 180
Hanna, Wilson C., second specimen of the dovekie from Alaska, 338; turkey vulture nesting in Pima County, Arizona, 419
Harpagus, 178–179
bidentatus, 178
diodon, 178–179
Harrison, C. J. O., notes on the behavior of the scaly dove, 450
Hartman, Frank A., and Brownell, Katharine A., lipids in the locomotor muscles of birds, 403
Hawfinch, 220
Hawk, Broad-winged, 404
Cooper, 178
Harlan, 98
Hawaiian, 342
Marsh, 116
Red-tailed, 98
Sparrow, 112, 179, 342
Swainson, 266
Hawk-Eagle, Ornate, 505
Heliornis fulica, 404
Helmintheros vermivorus, 218
Hemignathus lucidus hanapepe, 180
procerus, 180

Heron, Black-crowned Night, 417
Boat-billed, 403–404
Great Blue, 98
Green, 208
Heterocercus, 346–348
aurantiivertex, 346
flavivertex, 346, 348
linteatus, opp. 345, 346–348, 350
luteocephalus, 346, 350
Himatione sanguinea sanguinea, 180
Hirundo rustica, 212
rustica gutteralis, 419
Hoffmann, Robert S., and Hand, Ralph L., recent shorebird records for Montana, 180
Holoquiscalus, 58, 68
Honeycreeper, Blue, 201, 217, 218
Red-legged, 403, 406
Shining, 403, 406
Honeyeater, White-naped, 217
Hornbill, Casqued, 211
Crowned, 200, 202, 210
Red-and-White-billed, 211
Howell, Thomas R., an early reference to torpidity in a tropical swift, 505
Howell, Thomas R., and Bartholomew, George A., temperature regulation in Laysan and black-footed albatrosses, 185
Hummingbird (see also Mountain Gem)
Allen, opp. 3, 20–21, 23, 507
Anna, opp. 3, 10, 12, 15, 16, 20–21, 23
Black-chinned, opp. 3, 3, 8–12, 15
Broad-tailed, opp. 3, 3, 8, 100, 507
Calliope, opp. 3, 13–16, 21
Costa, opp. 3, 3, 10, 12–15
Lucifer, 10
Mexican Violet-eared, 323
Ruby-throated, 10, 323, 507
Rufous-tailed, 396, 405
Scaly-breasted, 405
Violet-bellied, 405
Humphrey, Philip S., and Clark, George A., Jr., pterylosis of the mallard duck, 365
Hylocichla fuscescens, 215
minima, 215
mustelina, 215
ustulata, 215, 406, 410

I

Icterus galbula, 277, 324
spurius, 220
Iiwi, 180
Io, 342
Iridoprocne bicolor, 212, 326
Ixobrychus exilis, 404

J

Jacana spinosa, 404
Jaçana, American, 404, 407
Jackdaw, 200, 212
Jaeger, Parasitic, 508
Pomarine, 342
Jay, Blue, 213
Brown, 203, 208, 212
Mexican, 213, 234, 242–243
Scrub, 148, 213, 234, 237–239, 244, 331
Steller, 143–144, 147
Tufted, 213
Unicolored, 243
Johnson, Ned K., and Banks, Richard C., a review of North American hybrid hummingbirds, 3
Johnson, Oscar W., reproductive cycle of the mallard duck, 351
Johnston, David W., salivary glands in the black swift, 338; timing of annual molt in the glaucous gulls of northern Alaska, 474
Johnston, Richard F., population movements of birds, 386
Junco hyemalis, 137, 509
hyemalis hyemalis, 183
oreganus, 183, 220, 357
Junco, Oregon, 183, 205, 220
Slate-colored, 137, 183, 509
Junglefowl, Red, 101, 107

K

King, James R., the bioenergetics of vernal premigratory fat deposition in the white-crowned sparrow, 128
Kingbird, Eastern, 218, 283
Western, 266
Kingfisher, Amazon, 403, 405
Green, 403, 405
Ringed, 405, 407
Kite, Black-shouldered, 200, 204, 209
Double-toothed, 178
Gray-headed, 178
Hook-billed, 403–404, 407
White-tailed, 178
Kittiwake, 334–335
Black-legged, 476
Knot, 180

L

Lagopus scoticus, 282
Lampornis castaneoventris, 405
Lanius ludovicianus, 148
Lanyon, Wesley E., specific limits and distribution of ash-throated and Nutting flycatchers, 421
Lark, Horned, 266, 284, 415
Larus argentatus, 324
californicus, 339, 356, 476
glaucescens, 457
hyperboreus, 414, 474–478
novaehollandiae, 262
occidentalis, 415
ridibundus, 101
Laterallus albigularis, 404
leucopyrrhus, 209

Leopold, Aldo, and Eynon, Alfred E., avian daybreak and evening song in relation to time and light intensity, 269
Lepidocolaptes affinis, 405
Leptodon, 178
Leptotila cassinii, 404
rufinucha, 404
verreauxi, 404
Leucophoyx thula, 404
Levy, Seymour H., two new birds recorded for Arizona, 98
Linnet, 214, 220
Locke, Louis N., sparrow hawk feeding on dragonflies, 342
Longspur, Lapland, 147
Lophoceros deckeni, 211
melanoleucos, 210
Lophortyx californicus, 97, 294–303, 314, 340
gambelii, 95–97
Lophotriccus pileatus, 406
Loxops coccinea caeruleirostris, 179
maculata bairdi, 179
parva, 180
virens stejnegeri, 180
Lunda cirrhata, 415, 457
Lybius albicauda, 211

M

Magpie, Black-billed, 112
Magpie-Jay, White-throated, 203, 213
Malurus, 210
amabilis, 216
cyaneus, 216
lamberti, 216
splendens, 216
Manacus, 345, 349
manacus, 345, 348–350
vitellinus, 345, 406
Manakin, Golden-crowned, 406
White-ruffed, 403, 406
Mannikin, Black-headed, 218
Rufous-backed, 218
Martin, Gray-breasted, 403, 406
House, 201, 212
Purple, 65, 200–203, 212
Sand, 212
Massornis, 348
McCabe, Robert A., the selection of colored nest boxes by house wrens, 322
Meadowlark, Eastern, 281, 284–285
Western, 418
Megapodius freycinet, 209
Megarhynchus pitangua, 406
Melanitta deglandi, 209
Melithreptes lunulatus, 217
Melospiza georgiana ericrypta, 183
georgiana georgiana, 183
melodia, 220, 271, 387, 507
Merganser, Red-breasted, 265
Mergus, 380
serrator, 265
Merlin, 178
Michener, Martin C., and Stein, Robert C., least flycatchers in northwestern Washington and central British Columbia, 181
Micrastur ruficollis, 404, 500
Miller, Alden H., a review of Hummingbirds, by Crawford H. Greenewalt, 100; molt cycles in equatorial Andean sparrows, 143; a review of the Kirtland's warbler, by Harold Mayfield, 268
Miller, Loye, birds from the Miocene of Sharktooth Hill, California, 399
Mimus polyglottos, 220, 266
Mniotilta varia, 217
Mockingbird, 220, 266
Moho braccatus, 179
Molothrus, 58, 68
ater, 58, 61, 69, 183, 220, 410
Momotus momota, 499
momota conexus, 405, 407
momota lessonii, 405, 407
Moorhen, 202, 209
Morejohn, G. Victor, and Genelly, Richard E., plumage differentiation of normal and sex-anomalous ring-necked pheasants in response to synthetic hormone implants, 101
Morus, 401
bassana, 401
serrator, 401
vagabundus, 399, 401
Motacilla alba, 206, 216
capensis, 217
cinerea, 217
flava, 324
Motmot, Blue-crowned, 405–406
Mountain Gem, White-throated, 405
Murre, 204
Common, 209, 411–412, 415
Murrelet, Ancient, 468
Marbled, 456
Muscicapa hypoleuca, 216
luteocephala, 345–346
striata, 214
Myiarchus, 421, 439, 445, 447
cinerascens, 421–449
cinerascens cinerascens, 421–425, 428–432, 439, 441–443, 445, 447
cinerascens flavidior, 422
cinerascens mexicanus, 422, 424, 433
cinerascens nuttingi, 422
cinerascens pertinax, 421, 423–425, 428–433, 441, 443, 447
crinitus, 214, 281, 424
inquietus, 421–422
nuttingi, 421–449
nuttingi flavidior, 424, 426–434, 441, 444, 447
nuttingi inquietus, 421–422, 424, 426–432, 434, 439, 441–447
nuttingi nuttingi, 421, 426, 428–432, 434, 441, 444, 447
nuttingi vanrossemi, 422, 424, 428

tuberculifer, 424, 437, 439, 447
tyrannulus, 421, 424, 431, 447
tyrannulus cooperi, 443
yucatanensis, 424, 437, 439
Myioborus miniatus, 406
Myiodynastes maculatus, 178, 406
Myiopagis viridicata, 406
Myiopsitta monachus, 210
Myrmotherula axillaris, 207

N

Nighthawk, Common, 278, 288–289
Lesser, 403, 405–406
Nightjar, 210, 278, 288–289
Nukupuu, 180
Nuthatch, Brown-headed, 202–203, 214
European, 205, 214
Pygmy, 202–203, 214
Red-breasted, 410
Nuttallornis borealis, 410
Nyctibius griseus, 405
Nycticorax nycticorax, 417
Nyctidromus albicollis, 405

O

Oceanodroma homochroa, 414
leucorhoa beali, 414
Odontophorus guttatus, 404
Oena capensis, 452–453, 454
Oenanthe oenanthe, 216
Oidemia nigra, 418
Oldsquaw, 418
Omao, 179
Oo, Kauai, 179
Oporornis, 349
agilis, 410
formosus, 218
philadelphia, 349
tolmiei, 349
Orians, Gordon H., social stimulation within blackbird colonies, 330
Oriole, Baltimore, 277, 281, 284, 324
Orchard, 220
Oropendola, Chestnut-headed, 406
Ortalis garrula, 404
Otus asio, 290
choliba, 405
Ou, 180
Ovenbird, 206, 217–218, 283, 410–411
Owl, Barn, 403, 405, 407
Black and White, 403, 405, 407
Burrowing, 414
Ferruginous, 483
Horned, 469
Screech, 290
Striped, 405
Tawny, 289
Tropical Screech, 405
Oystercatcher, 182
Black, 414

P

Palm-Chat, 204, 217
Panyptila sancti-hieronymi, 505
Parakeet, Gray-breasted, 204, 210
Orange-chinned, 404
Parauque, 405–406
Parkes, Kenneth C., intergeneric hybrids in the family Pipridae, 345
Parrot, Brown-hooded, 404, 407
Red-lored, 404
Partridge, Chukar, 111–127
Hungarian, 294
Red-legged, 111, 113, 115–116
Partridge, William H., Accipiter pectoralis, a synonym of Accipiter poliogaster, 505
Parula, 349
Parus ater, 214
bicolor, 213
caeruleus, 213, 323
gambeli, 213
major, 213, 323
Passer domesticus, 52, 101, 215, 218, 323, 338–340, 356, 387, 410, 454
Passerculus sandwichensis, 80, 97, 418
sandwichensis nevadensis, 97
Passerella iliaca, 507
Passerina, 341
amoena, 341
cyanea, 220, 281, 341, 406
Payne, Robert B., growth rate of the lens of the eye of house sparrows, 338
Pearson, Oliver P., flight speeds of some small birds, 506
Pedioecetes phasianellus, 171
Pelecanus erythrorhynchus, 209
occidentalis, 414
Pelican, Brown, 414
White, 207, 209
Penguin, Adelie, 200
Chinstrap, 200
Emperor, 200
Perdix perdix, 294
Pernis celebensis, 179
Petrel, Ashy, 414
Hawaiian, 261
Leach, 414
Scaled, 417
Petrochelidon pyrrhonota, 212
Pewee, Eastern Wood, 273, 281, 284
Phacellodomus rufifrons, 212
Phaeochroa cuvierii, 405
Phaeornis obscurus myadestina, 179
palmeri, 179
Phaethon rubicauda, 261
Phalacrocorax auritus, 414
carbo, 209
olivaceus, 404
pelagicus, 414
penicillatus, 414
Phalaenoptilus nuttallii, 289
Phalarope, Red, 97–98

Phalaropus fulicarius, 97–98
Pharomachrus mocinno, 405
Phasianus, 108
colchicus, opp. 101, 101–110, 112, 270–271, 280, 294, 340, 361
Pheasant, Ring-necked, opp. 101, 101–110, 112, 115, 270, 279–282, 284, 291, 294, 340, 361
Pheucticus ludovicianus, 220, 406
melanocephalus, 220
Philetairus socius, 218
Philohela minor, 279, 286
Phloeoceastes melanoleucos, 405
Phoebe, Black, 415, 453
Eastern, 205–206, 212
Say, 266
Phoebetria palpebrata, 261
Phoenicopterus antiquorum, 200
ruber, 209
Phoenicurus ochrurus, 216
phoenicurus, 282
Phylloscopus borealis, 417
borealis examinandus, 417
trochilus, 206, 214
Pica pica, 112
sieberii, 241
Piculet, Olivaceous, 405
Piculus rubiginosus, 405
Picumnus olivaceus, 405
Pigeon, Domestic, 210
Ruddy, 404
Scaled, 404
White-naped, 404, 407
Pinicola enucleator, 419
enucleator leucura, 419
Pintail, 361
Pionopsitta haematotis, 404
Pipilo erythrophthalmus, 220, 272, 313–321
fuscus, 220, 507
Pipit, Meadow, 324
Tree, 217
Pipra, 345–349
anomala, opp. 345, 346–348, 350
aureola, 345, 347–348, 350
aureola aurantiicollis, opp. 345, 346
erythrocephala, 345, 348–350
fasciicauda, 345, 350
heterocerca, 345, 350
Piranga olivacea, 219
rubra, 406
Pitelka, Frank A., new wildlife ranges in Alaska, 99; comments on types and taxonomy in the jay genus Aphelocoma, 234
Platalea, 452
Plautus alle, 338
Plectrophenax nivalis, 147
Plover, Black-bellied, 180
Kentish, 203, 209
Semipalmated, 181
Snowy, 209
Podiceps auritus cornutus, 227
caspicus californicus, 227
dominicus, 404
grisegena holböllii, 227
Podilymbus podiceps, 264
podiceps podiceps, 227
Polioptila plumbea, 216
Poor-will, 289
Potoo, Common, 405
Presbychen abavus, 401
Prinops plumata, 217
poliocephalus, 217
Progne chalybea, 406
subis, 65, 212
Prunella modularis, 214
Psaltriparus melanotis, 213
minimus, 214
Psilorhinus mexicanus, 212
Psittirostra psittacea, 180
Pterodroma inexpectata, 417
phaeopygia, 261
Pteroglossus frantzii, 206, 405
torquatus, 211, 405
Pteronetta hartlaubi, 374
Ptilonorhynchus violaceus, 324
Ptychoramphus aleutica, 415, 456
Puffin, Tufted, 415, 457–458, 470
Puffinus, 399, 401
diatomacus, 401
griseus, 401
inceptor, 399–401
leucomelas, 261
mitchelli, 400–401
opisthomelas, 401
pacificus, 468
priscus, 399–401
Pygoscelis adeliae, 200
antarctica, 200
Pyromelana franciscana, 101
Pyrrhuloxia, 246–256
sinuata, 246–256

Q

Quail, Bobwhite, 97, 113
California, 97, 183, 294–303, 314, 340
European, 451
Gambel, 95–97
Japanese, 403–404, 407–408
Scaled, 294, 300, 340
Spotted Wood, 404
Quelea quelea, 218
Querula purpurata, 406
Quetzal, 405
Quiscalus, 58, 61, 79
quiscula, 52, 78, 218

R

Rail, 209
Gray-necked Wood, 404
Raitt, Ralph J., Jr., plumage development and molts of California quail, 294
Ramphastos, 179
swainsonii, 405

Ramphocelus passerinii, 219
Raven, 200, 207
Common, 212, 474
Recurvirostra, 402
americana, 402
avosetta, 209
Redstart, 282
American, 205, 218, 410, 411
Black, 216
Slate-throated, 403, 406
Rhinoptynx clamator, 405
Rhynchocyclus brevirostris, 406
Richardson, Carl, tricolored blackbirds nesting in Jackson County, Oregon, 507
Richardson, Charles H., and Richardson, Alice I., golden-winged warbler in Southern California, 504
Richardson, Frank, breeding biology of the rhinoceros auklet on Protection Island, Washington, 456
Richardson, Frank, and Bowles, John, records of the rarer native forest birds of Kauai, Hawaii, 179
Richmondena cardinalis, 219, 246–256, 270, 275
phoenicea, 246
Rickard, W. H., notes on bird nests found in a desert shrub community following nuclear detonations, 265
Riparia riparia, 212
Rissa tridactyla, 334, 476
Robin, American, 203, 205–207, 210, 215, 219–220, 271–272, 275, 277–278, 281–285, 288, 290–291
European, 137, 205–207, 213, 215–216, 270, 279, 288
Mountain, 406–407
Roest, Aryan I., bird records from San Luis Obispo County, California, 508
Rook, 279
Roper, Laren A., and Ryder, Ronald A., recent waterfowl records for Colorado, 418
Ryder, Ronald A., and Roper, Laren A., recent waterfowl records for Colorado, 418

S

Sabrewing, Violet, 405
Salpinctes obsoletus, 410
Saltator albicollis, 406
maximus, 219
Saltator, Buff-throated, 203, 219
Streaked, 406
Sanderling, 181
Sandpiper, Baird, 181
Curlew, 182
Least, 181, 183
Semipalmated, 181, 183
Western, 181, 183
Sapayoa, 348
Sapsucker, Williamson, 205, 213
Sayornis nigricans, 415, 454
phoebe, 212
saya, 266
Scardafella inca, 450, 455
squammata, 450–455
squammata ridgwayi, 450
Scaup, Lesser, 209, 404, 407
Schiffornis, 348
Scolecophagus carolinus, 165
Scoter, Common, 418
White-winged, 209
Seedeater, Yellow-bellied, 390–398
Seiurus aurocapillus, 206, 217, 283
aurocapillus aurocapillus, 410
Selander, Robert K., supplemental data on the sex ratio in nestling boat-tailed grackles, 504
Selander, Robert K., and Giller, Donald R., analysis of sympatry of great-tailed and boat-tailed grackles, 29
Selasphorus, 3, 22, 26
alleni, 17–18
floresii, 17–18, 20
platycercus, 3–10, 17, 22–25, 507
rufus, 17–18, 22–25
sasin, 5, 7, 17–26, 507
Selsor, C. Jackson, and Stott, Ken, Jr., association of trogons and monkeys on Barro Colorado, 508
Semnornis frantzii, 405
Setophaga, 349
ruticilla, 218, 410
Shearwater, Wedge-tailed, 468
White-faced, 261
Sheld-duck, 200
Shrike, Loggerhead, 148
Spectacled, 217
White-crowned, 217
White Helmet, 217
Sialia, 201
currucoides, 215
mexicana, 215
sialis, 215, 281
Sieberocitta, 243
Siskin, Pine, 415
Sitta canadensis, 410
europaea, 214, 323
pusilla, 214
pygmaea, 214
Skutch, Alexander F., helpers among birds, 198
Skylark, European, 418
Snipe, Swinoe, 417
Sparrow, Andean, 143–161
Black-throated, 266
Brewer, 266
Chipping, 202, 218–220, 281, 284
English, 323
Field, 206, 220, 273–277, 281–285, 291, 403, 406
Fox, 507
Golden-crowned, 507
Green-backed, 406
Hedge, 214
House, 52, 101, 215, 218, 338–340, 356, 387, 410–411, 454
Savannah, 80, 97, 418

Song, 204, 206–207, 219–220, 271, 276, 281–285, 387, 507
Swamp, 183
Tree, 137, 509
White-crowned, 91, 128–142, 356–357, 507
White-throated, 137
Speotyto cunicularia, 414
Spermestes nigriceps, 218
Sphyrapicus thyroideus, 205, 213
Spinetail, Slaty, 405
Spinus pinus, 415
psaltria, 410
Spizaetus lanceolatus, 179
ornatus, 505
Spizella arborea, 137, 509
breweri, 266
passerina, 220, 281
pusilla, 220, 273, 406
Sporophila gutturalis, 390
nigricollis, 390–398
Squatarola squatarola, 180
Starling, 55, 112, 183, 205, 214, 279, 508
Stearns, Edwin I., dragonfly "attacks" Hawaiian hawk, 342
Stein, Robert C., and Michener, Martin C., least flycatchers in northwestern Washington and central British Columbia, 181
Stellula, 3, 22, 26
calliope, 5, 7–9, 13–17, 21–26
Stercorarius parasiticus, 508
pomarinus, 342
Sterna forsteri, 341
paradisaea, 209
Stint, Little, 182
Temminck, 182
Stokes, Allen W., voice and social behavior of the chukar partridge, 111
Stott, Ken, Jr., and Selsor, C. Jackson, association of trogons and monkeys on Barro Colorado, 508
Streptopelia, 452, 455
chinensis, 453
decaocto decaocto, 455
decaocto stoliczkae, 417
risoria, 455
roseogrisea, 455
Strix aluco, 289
Sturnella, 68–69
magna, 69, 281
neglecta, 69, 418
Sturnus vulgaris, 55, 112, 183, 205, 214, 279, 508
Sula dactylatra, 261
leucogaster, 209, 261
nebouxi, 401
Sungrebe, 404
Swallow, Amur Barn, 419
Bank, 212
Barn, 200–201, 212
Cliff, 212
European, 201
Papuan Wood, 217
Tree, 204–206, 212, 326
Violet-green, 212, 457
Swan, Whistling, 401
Swift, Black, 338
Chimney, 203, 210, 338
Greater Swallow-tailed, 505
White-throated, 505
Sylvia communis, 137, 216
Synallaxis brachyura, 405
Synthliboramphus antiquus, 468

T

Tachycineta thalassina, 212, 457
Tadorna tadorna, 200
Tanager, Bay-headed, 406
Blue, 219
Blue-gray, 406
Common Bush, 406
Golden-masked, 201–203, 205, 216, 218, 406
Plain-colored, 219
Scarlet, 219
Scarlet-rumped Black, 203, 217, 219
Speckled, 203, 219
Summer, 406
Yellow-browed, 219
Tanagra imitans, 207
Tangara gyrola, 406, 486
inornata, 219
chrysophrys, 219
larvata, 218, 406
Tangavius aeneus milleri, 183
Teal, Blue-winged, 404
Teleonema, 345
filicauda, 345, 350
filicauda filicauda, 345
Telmatodytes plaustris, 87
Tern, Arctic, 203, 209
Black, 341
Forster, 341
White, 466
Thamnophilus doliatus, 406
Thompson, Max C., the flight speed of a red-breasted merganser, 265
Thornbird, Rufous-fronted, 204, 212
Thrasher, Brown, 277, 281
California, 340
Thraupis episcopus, 219
virens, 406
Thrush, Gray-cheeked, 215
Olive-backed, 406
Small Kauai, 179
Song, 205, 216
Swainson, 215, 410–411
Wood, 203–204, 215
Thryomanes bewickii, 205, 220
Thryothorus ludovicianus, 214
modestus, 406
Tiger-heron, Banded, 404
Tigrisoma lineatum, 404
Tinamou, Little, 404, 407

Tit, Blue, 205, 213
Coal, 214
Great, 203, 213–214
Long-tailed, 204, 213
Titmouse, Tufted, 213
Tityra semifasciata, 406
Tityra, Masked, 406
Toucan, Chestnut-mandibled, 405, 407
Towhee, Abert, 254
Brown, 205–206, 220, 254, 507
Rufous-sided, 206, 220, 272, 276, 279, 281–282, 284, 313–321
Toxostoma redivivum, 340
rufum, 277
Tripsurus chrysauchen, 211
Trochilus, 11
anna, 17
floresii, 17
rufus, 17
violajugulum, 10–13
Troglodytes aëdon, 87, 215, 271, 276, 322–329, 370
musculus, 215
troglodytes, 214, 270
Trogon massena, 508
rufus, 405
strigilatus, 405
violaceus, 405
Trogon, Black-throated, 405
Slaty-tailed, 508
Violaceous, 405
White-tailed, 405, 407
Tropic Bird, Red-tailed, 261
Turdoides striatus, 214
Turdus ericetorum, 205, 216
merula, 203, 215, 270
migratorius, 210, 215, 271, 278
plebejus, 406
Tyrannus tyrannus, 218, 284
verticalis, 266
Tyrant, Scale-crested Pygmy, 406
Tyto alba, 405

U

Uria aalge, 209, 415

V

Veery, 215
Vermivora, 349
chrysoptera, 349, 504
pinus, 349
Vestiaria coccinea, 180
Vireo gilvus, 281
olivaceus, 218, 410
Vireo, Red-eyed, 218, 410
Warbling, 281
Volatinia jacarina, 391
Vulture, Black, 200, 207, 212
Turkey, 419

W

Wagtail, Cape, 217
Gray, 205, 217
Pied, 206–207, 216
Yellow, 324
Walkinshaw, Lawrence H., and Zimmerman, Dale A., range expansion of the Brewer blackbird in eastern North America, 162
Wallace, William M., scaled petrel in Oregon, 417
Warbler, Arctic Willow, 417
Black-and-White, 206, 217
Chestnut-sided, 410, 411
Connecticut, 410
Golden-winged, 504
Great Reed, 282
Jack Pine, 268
Kentucky, 203, 218
Kirtland, 268
Prairie, 419
Willow, 206, 214, 216
Worm-eating, 206, 217–218
Yellow, 206, 220
Weaver, Black-faced, 218
Red-billed, 218
Social, 204, 218
Weeden, Judith S., and Weeden, Robert B., winter record of a tree sparrow in central Alaska, 509
Wheatear, 203, 216
Whip-poor-will, 289
Whitethroat, 137
Common, 216
Wilhoft, Daniel C., birds observed during two crossings of the Pacific Ocean, 257
Williams, Laidlaw, indigo bunting at Carmel, California, 341
Willis, Edwin, prairie warbler off the Pacific coast of Guatemala, 419; a study of nesting antanagers in British Honduras, 479
Wolf, Larry L., and Grefe, Robert E., Brewer blackbird nesting in eastern Michigan, 182
Woodcock, American, 279, 285–287, 290–291
Woodhewer, Buff-throated, 405, 407
Spot-crowned, 405
Woodpecker, Acorn, 211
Black-cheeked, 405, 407
Crimson-crested, 405
Golden-naped, 211
Golden-olive, 405, 407
Lineated, 405, 407
Red-crowned, 405, 407
Wren, Banded-backed, 203, 208, 214
Bewick, 205, 220
Blue Fairy, 203, 216
Cactus, 87–94
Carolina, 205, 214
European, 214, 216, 270, 275–276, 278, 282, 289
House, 87, 271–272, 275–277, 281–282, 284–285, 291, 322–329, 370
Long-billed Marsh, 87

Lovely Fairy, 216
Northern House, 206, 215
Plain, 406
Rock, 410
Short-billed Marsh, 172
Splendid Fairy, 216
Southern House, 202, 215
Variegated Fairy, 216
Winter, 203, 205, 214

X

Xiphorhynchus guttatus, 405

Y

Yellowthroat, 281–282, 284–285, 410–411

Z

Zarhynchus wagleri, 406
Zenaida asiatica, 205, 210
Zenaidura macroura, 210, 271, 324
Zimmerman, Dale A., and Walkinshaw, Lawrence H., range expansion of the Brewer blackbird in eastern North America, 162
Zonotrichia, 131, 148, 160, 279
albicollis, 137, 139–140
atricapilla, 160, 507
capensis, 143–161
leucophrys, 91, 160, 356, 507
leucophrys gambelii, 128–142

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